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SOME OBSERVATIONS ON THE DEVELOPMENT OF THE VENTRAL PANCREAS IN MAN

By P. N. B. ODGERS

Department of Human Anatomy, Oxford University

Since 1888, when Phisalix first demonstrated that the human pancreas arises by a ventral outgrowth in addition to the dorsal diverticulum already described by His, two details with regard to its origin have been matters of doubt and disagreement and still remain so. These may be briefly put in the form of two questions:

(1) Is the ventral pancreatic outgrowth in man single or paired?

(2) If it is the latter, do both portions of it share in the formation of the adult gland?

The accounts given in different standard text-books suggest varying answers to these questions. Keith and Arey in their text-books and Lewis, who wrote the account of the development of the pancreas in Keibel and Mall, describe a single ventral formation, while in Buchanan's and Cunningham's manuals, "the ventral diverticulum is at first double, right and left outgrowths arising from the liver bud; the left formation quickly disappears." A similar view is taken by McMurrich, who writes "of the ventral outgrowths, that upon the left side may be wanting, or, if formed, early disappears. Broman describes a single ventral anlage, "which is derived from paired thickenings of the wall of the foregut."

If one refers to the original investigations upon which these statements are founded, one wonders if they quite fairly reflect the weight of evidence. Felix, in 1892, was the first to describe two ventral outgrowths, a right one and a rudimentary left one: both of these, according to him, blend with each other and both form pancreas. This observation was confirmed by Zimmermann, Jankelowitz, Piper, Opie, Ingalls, Debeyre and Siwe. Jankelowitz published his account in 1895, and in 1907 his views were in all essentials re-stated by Ingalls, who examined the same specimen. In a 4·9 mm. embryo—I am quoting Ingalls' paper—they described the ventral pancreas as originating by two outgrowths, one from either side of the junction of the hepatic diverticulum and the gut, which united with each other caudal to the former; of these the right was the better developed. Both outgrowths possessed a small lumen, which was not always distinct. If followed cranialwards, these lumina appeared to join the lateral borders of the choledochus: if followed caudally, they blended and this common lumen could be traced to the caudal end of the fused outgrowths. Similarly, Piper, in a 6·8 mm. embryo, in two sections

found that the ventral pancreas showed two lumina. Siwe in 1927 found in 2·5 and 3 mm. embryos two entirely separate ventral anlages in the gut wall, one on either side of the hepatic outgrowth. He suggests that both of these blend and that both form gland substance.

Helly and Kollman both published cases of paired ventral pancreases which have not fused. It is worth while quoting Helly's description in some detail because, as far as I know, it is on this evidence, and this alone, that the statement so commonly made, that the left outgrowth atrophies, is founded. He studied an embryo, 11 mm. in length, which he said corresponded in the development of its organs to the 7·5 mm. embryo of His. The ventral pancreas arose in this case from the bile duct 20μ above its opening into the duodenum in the form of right and left anlages, of which the right was the more considerable. He could not see any actual coalescence between the two, which were always separated by the choledochus: this independence was distinctly shown in his reconstruction. Microscopically he found a great difference between the two. While the right one appeared to be actively growing, with a distinct lumen and recognisable alveoli, the left one gave him the impression of degeneration with smaller and less distinct cells: in this part no lumen could be distinguished. He concluded that the significance of this observation was that it filled the gap between the view that there were two ventral outgrowths in man and the idea that there was only one. It is to be expected, he says, that in embryos older than four weeks the left anlage has already disappeared.

To have such non-fusion of the ventral outgrowths at this stage—whether it be regarded as a 7·5 or as an 11 mm. embryo—is so unusual, that Lewis maintains that the specimen is properly regarded as exceptional, and Helly's deduction from this, that in much younger embryos the left anlage has already degenerated, appears unwarranted.

Thyng in 1908 described the condition of the pancreas found in embryos 7·5 mm. and 13·6 mm. in length. From these he concluded that "the present study has shown no sufficient reason for subdividing the ventral pancreas into two independent lateral parts." This view was adopted by Lewis in Keibel and Mall's *Manual*, who wrote: "in other embryos, between 7·5 and 11 mm. in length, including seven specimens in the Harvard Collection, the ventral pancreas appears as a single outgrowth." Again, it must be mentioned that Keibel and Elze, who re-examined the Jankelowitz 4·9 mm. embryo, disagreed with his interpretation and they stated "that it is very questionable whether two outgrowths are present; to us there appears to be only one." Further, of the four other embryos between 4 and 5 mm. described in their *Normentafeln*, in only one of them did they see any indication of a paired origin for the ventral pancreas.

My own observations were made on embryos of 5 mm., 7·1 mm., 11·4 mm., 14 mm. and 23 mm. in length: a reconstruction model of the pancreas was made in each case.

5 mm. embryo. Here the ventral pancreas is seen filling up the angle that the hepatic outgrowth makes with the bowel and partially encircling the latter. It is horseshoe-shaped with a left limb smaller than the more projecting right limb, but commencing somewhat cranial to the latter. The whole bilobed outgrowth already appears as if it were being drawn out dorsalwards and to the right (fig. 1). If sections (10μ) of this are examined, one finds that the ventral pancreas extends through seven sections in all. The left "lobe" appears first, two sections cranial to the right one, as a projection from the most caudal part of the opening of the bile duct into the gut (Plate I, fig. 4). If one looks at a section midway through this pancreas, one sees a definitely

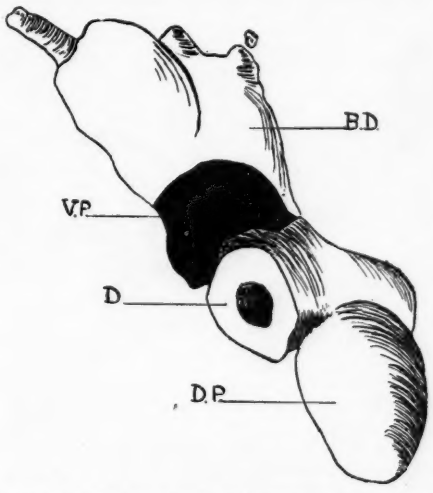

Fig. 1. Drawing of a model of the duodenum and pancreas, viewed from below, in a 5 mm. embryo. *D.* duodenum; *B.D.* bile-duct; *V.P.* ventral pancreas; *D.P.* dorsal pancreas.

bilobed mass and in this, I suggest, are two lumina, of which the left is the larger and the more obvious (fig. 5). In the next section below this one (fig. 6) these two lumina are apparently fusing into one—a fine septum is seen dividing the common lumen—and the rest of the pancreas caudal to this is solid. Traced cranialwards, in the next section cranial to fig. 5 the right lumen has disappeared, but I can trace the left lumen through this one and the section next above it to open, I think, into the bile duct (fig. 4).

7·1 mm. embryo. The ventral pancreas here extends over three sections (10μ) and is seen as a solid outgrowth from the right or dorsal side of the bile duct, which commences 70μ cranial to the latter's opening into the gut (fig. 2). This outgrowth projects in a dorsal direction and is exactly parallel to the dorsal pancreas. The only suggestion of any lumen I can see in it is at its commencement, where the lumen of the bile duct appears to be slightly

drawn out towards it in the form of a crescent. In neither the 5 mm. nor in the 7·1 mm. stage could I see any difference between the cells of the left or of the right portions of the outgrowths, suggesting that any of it was degenerating.

11·4 *mm. embryo.* Fig. 3 shows a drawing of the ventral pancreas from a photograph of a reconstruction at this stage. In it one can see two ventral pancreatic ducts, one cranial to, and much smaller than the other: these run parallel to each other and both open, one immediately above its fellow, into the common bile duct. I attempted to trace up these ducts to discover if they drain two distinct lobes of the ventral pancreas, but they both appear to issue from a fused mass of gland.

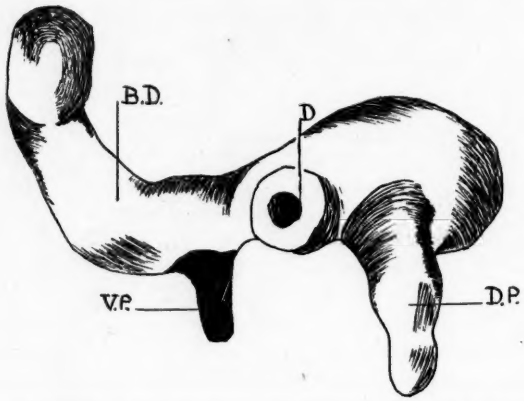

Fig. 2. Drawing of a model of the duodenum and pancreas, viewed from below, in a 7·1 mm. embryo. *D.* duodenum; *B.D.* bile-duct; *V.P.* ventral pancreas; *D.P.* dorsal pancreas.

These few observations of mine fall, I think, into line pretty well with those of previous observers. In the youngest, 5 mm. embryo, the ventral pancreas appears bilobed with two lumina: in the older, 7·1 mm. stage, there is but a single outgrowth, which appears to correspond to the right horn of the earlier one. This agrees entirely with Thyng's description of a slightly older 7·5 mm. embryo and with Lewis, who found a similar single outgrowth in the seven embryos of the Harvard Collection between 7·5 and 11 mm. in length. It is, however, hardly fair to assume from these later embryos, that the outgrowth was originally unpaired, and it is rather in the interpretation of the earlier stages that differences of opinion arise. As Siwe says, "In mehreren anderen Fällen kann man eine Andeutung zu Paarigkeit sehen—wenn man so will (oder auch nicht, wenn man nicht will)." I would suggest that there are originally two separate outgrowths, right and left, which fuse very early. Of these the right is the more extensive. M. Tribe, in describing the development of the pancreas in marsupials, shows that the right ventral

outgrowth contributes four times as much as does the left to the adult gland and remarks "in man the two ventral outgrowths are of such unequal size that one of them has frequently been overlooked altogether." This more extensive right lobe drags its fellow to the right and dorsally. This appearance has been noted already as beginning in the 5 mm. stage and its persistence leads to the appearance of a single outgrowth, which, by the growth of the bile duct, is entirely divorced from the bowel wall. The lumina I describe in the 5 mm. stage are exactly similar to those figured by Jankelowitz in his 4·9 mm. embryo. While I realise that too much stress should not be laid upon them or upon their apparent fusion, Siwe, I think, rightly says "that one can hardly dismiss the question as Helly does, when he believes that two

Fig. 3. Drawing of a model of the duodenum and ventral pancreas, viewed from the right side, in an 11·4 mm. embryo. *D.* duodenum; *B.D.* bile-duct; *V.P.* ventral pancreas; *W* and W_1 mark the two ventral pancreatic ducts.

lumina can occur in any homogeneous anlage. Helly has not shown that the anlage was ever originally solid and further these lumina appear so early that one rather has reason to assume that no compact stage preceded them. The other possibility that a lumen, branched to right and left, could be the primary formation is at least as much justified." The duplication of the ventral duct, which I found in my 11·4 mm. embryo, is most readily explained by a delayed fusion of two separate outgrowths. I would suggest that the more slender and more cranial of the ducts represents the original left ventral proliferation, while the larger and more caudal of the two is formed by the larger right outgrowth.

Again, fusion of the two ventral elements seems a more probable explanation of the appearances noted than to assume that the left outgrowth atrophies. Debeyre in 1909 found the two ventral anlages in a 4·5 mm. embryo, but, as he could of course only find a single outgrowth in the 12 mm.

stage, assumed that the left proliferation early disappears. I have already pointed out that in Helly's 11 mm. embryo the apparent degeneration of one of the ventral masses, abnormally unfused at this age and entirely separated from each other by the bile duct, cannot be admitted as good evidence of the normal atrophy of one outgrowth.

Further, a paired origin for the ventral pancreas in Man should be expected from the way in which this is developed in other animals. In all vertebrates except Cyclostomes, it arises from the fusion of bilateral anlages (Siwe). Again, certain anomalous conditions in the adult are most easily explained in this way. Duplication of Wirsung's duct, which has been observed occasionally, would be the result of delayed fusion of the two separate outgrowths (Hasse), while the occurrence of an annular pancreas can be best ascribed to abnormally directed growth of the left ventral lobe, "when the left lobe tends to encircle the intestine instead of extending into the ventral mesentery" (Lewis).

Two other points arise out of an examination of the older 14 mm. and 23 mm. embryos. The time of fusion between the dorsal and the ventral pancreas must be variable. Keibel and Elze in the *Normentafeln* described them as uniting between the 12 and the 14 mm. stage. In my 14 mm. embryo, while there is considerable interlocking, it is quite easy to pick out the two portions—in fact, they are more distinct than in the earlier, 11·4 mm., one. Siwe mentions that fusion had not commenced in one embryo of 17 mm. Certainly in my 23 mm. specimen it was guesswork attempting to separate dorsal from ventral pancreas, which had completely joined together.

Lastly, an examination of the reconstructions from the 11·4 and the 14 mm. embryos suggests that the ventral pancreas must form much less of the fully developed gland than is often stated. I think it cannot be responsible really for more than the middle lateral part of its head, immediately about the terminal portion of Wirsung's duct.

SUMMARY AND CONCLUSIONS

Reconstruction models of the pancreas were made from human embryos 5, 7·1, 11·4, 14 and 23 mm. in length. In the 5 mm. embryo the ventral pancreas appears as a bilobed mass, in which two apparent lumina can be distinguished: this is replaced in the 7·1 mm. stage by a single outgrowth. These observations rather tend to support the view that the ventral pancreas in man is developed by two separate proliferations from the hepatic diverticulum, both of which, fusing early, may share in the formation of the adult gland. This view finds confirmation in the 11·4 mm. embryo examined. Here there is a duplication of the ventral duct, apparently due to delayed fusion of the two ventral anlages.

I should like to express my thanks to Prof. Arthur Thomson for much helpful advice and to Mr W. Chesterman for a great deal of assistance in preparing the reconstructions and for producing these microphotographs.

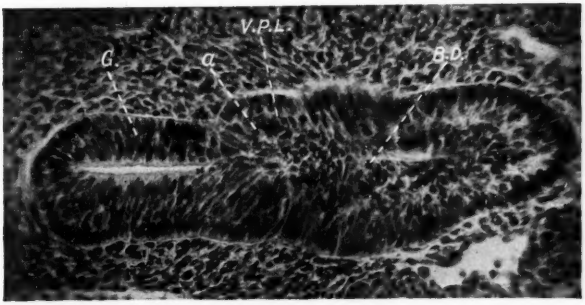

Fig. 4

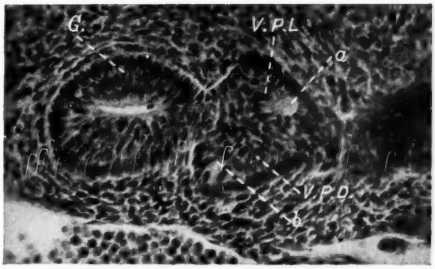

Fig. 5

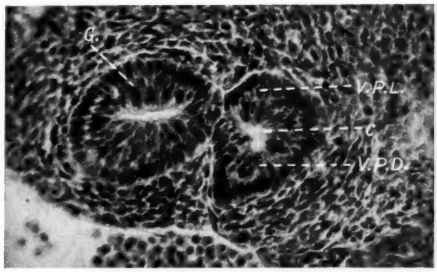

Fig. 6

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DESCRIPTION OF PLATE I

Fig. 4. Section through the caudal end of the hepatic outgrowth. *G.* gut; *B.D.* bile-duct; *V.P.L.* left ventral pancreas, showing at *a* an apparent lumen opening into the junction of the bile-duct with the duodenum. (× 200.)

Fig. 5. Section midway through the ventral pancreas. *G.* gut; *V.P.L.* and *V.P.D.* mark the bilobed ventral pancreas, in which at *a* and *b* are two separate lumina. (× 200.)

Fig. 6. Section immediately caudal to fig. 5. *G.* gut; *V.P.L.* and *V.P.D.* mark the ventral pancreas, in which at *c* there is a single lumen divided by a fine septum. (× 200.)

THE CELL MASSES IN THE FOREBRAIN OF *SPHENODON PUNCTATUM*

By ARCHIBALD DURWARD, M.B., Ch.B.

From the Department of Anatomy, University of Otago, New Zealand

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INTRODUCTION

So far back as 1897 Elliot Smith made observations on the cell masses in the brain of *Sphenodon* which gave this reptile a unique interest. Various writers since that date have cited his remarks and used his figures; some have had access to fresh material, but up to the present time no paper has appeared dealing with the detailed anatomy of the adult brain stained electively by modern methods to show cell masses.

Hines has given a brief account of the cell masses, but her paper was chiefly concerned with the development of the forebrain. Cairney as recently as 1926, working in the laboratory of Prof. C. Judson Herrick of Chicago, gave a lucid survey of the forebrain, but here again the study of cell masses was hampered by the paucity of material suitably stained for that purpose. Since that date more material has come to hand in this laboratory and has been prepared specially for the study of cell masses.

In the present paper the aim has been to present a complete and detailed account of the cell masses in the forebrain of *Sphenodon* rather than to determine the homologies of the various component nuclei. I have not been able to add anything further to Cairney's account of the olfactory bulb and peduncle; a description of these parts is, therefore, not included in the present

paper. A nomenclature corresponding largely with that adopted by Cairney has been used where possible; but in certain regions, e.g. the septum and thalamus, where this writer due to lack of suitable material was unable to unravel completely the nuclear arrangement, the usage of Huber and Crosby (1926) has been adopted where homologies seemed at all certain.

A definite drawback to the practical study of comparative neurology in New Zealand has been the inability of access to many of the more important papers dealing with the reptilian brain. For this reason the scope of the present paper has been largely confined to a pure description of the cell masses.

MATERIAL AND TECHNIQUE

The observations incorporated in this paper have been made on numerous series of adult brains stained by toluidin blue. The technique was one kindly proposed by Prof. G. Carl Huber, University of Michigan, Ann Arbor, and has in all cases given the utmost satisfaction. Six brains were cut transversely, one horizontally, and four in a sagittal plane. Besides this adult material several foetal brains were prepared by Huber's toluidin blue technique and cut in various planes. These, however, were not sufficiently early to add anything to what has already been so clearly described by Hines (1923) and Wyeth (1924).

In addition to such material electively stained by toluidin blue, I have had at my disposal numerous series stained by Weigert, Cajal, Ranson and Gurdjian methods and cut in all three planes. Although the study was not made on such fibre material, it was invaluable at times for confirmation of what was shown in cell preparations.

This study of the forebrain of *Sphenodon* is a continuation of the research programme instituted in the Anatomy Department of the University of Otago by Prof. W. P. Gowland. It is hoped ultimately to provide a complete description of the brain of this reptile and also of the brain of the New Zealand kiwi (*Apteryx australis*).

I have to acknowledge a just debt of gratitude to Dr Gowland, at whose suggestion I undertook this work and whose advice and encouragement I have at all times received.

CENTRES OF THE HEMISPHERE

The cortex cerebri

The cerebral cortex of *Sphenodon* is demonstrated with diagrammatic clarity in toluidin blue preparations, and in the figures accompanying this paper the cortex is shown in all its aspects. It forms a continuous sheet over the dorsal aspect of the hemisphere throughout its whole extent from the peduncular base rostrally back to the caudal pole. It also descends on both medial and lateral aspects of the hemisphere for varying distances in different regions.

Three cortical sheets are identifiable on the evidence of cell arrangement, viz. a medial hippocampal cortex, a lateral pyriform cortex, and an intervening one, the general cortex. Cell size, which apparently has been of use in other forms in distinguishing the three sheets of cortex, has not been found to lend any assistance in *Sphenodon*; nevertheless each sheet has quite distinctive features, which will be detailed under the appropriate headings.

Hippocampal cortex

Undoubtedly this is structurally the best organised and the most highly developed portion of the cortex cerebri, and presents remarkable constancy in appearance when traced throughout the length of the brain wall. It is composed of a continuous sheet of cells bent upon itself and lying in the adjacent portions of the medial and dorsal walls of the hemisphere. The longer limb generally occupies the medial wall, whilst the part bending over into the dorsal wall is shorter, particularly in the rostral part of the hemisphere.

The cells composing the hippocampal cortex are of medium size, are densely packed, and in general do not show much scattering into the adjacent white matter. At its ventral extremity the hippocampus becomes more slender and here, as a rule, the cells show some scattering towards the septum. There is no marked difference in cell size in different parts of the hippocampus; those at its ventral extremity are, if anything, slightly smaller than in the rest of the sheet, but the difference is so slight that one cannot fairly divide the hippocampus into dorsal and ventral portions on this criterion, as suggested by Elliot Smith (1910).

The position of the sheet in the brain wall is uniformly about midway between pial and ventricular surfaces, but ventrally it inclines towards the pia. Its ventral extremity coincides with the level of the fissura hippocampi (figs. 1–10).

As the hippocampal cortex is traced rostrally in transverse series it does not diminish so rapidly as does the cross-section of the hemisphere; thus this cortical sheet appears more conspicuous and of greater relative extent in the more rostral sections. The characteristic features of the column are, however, preserved well forwards towards the peduncle, although some loosening of its structure—a loss of compactness—is observable here (fig. 1). The vertical limb is decidedly the longer in the rostral part of the hemisphere.

Caudally from the level of the foramen of Monro the hippocampal cortex becomes reduced in extent and, as was the case in the most rostral sections, loses some of its sharp definition.

The general features of this cortical layer are well seen in horizontal sections. It is then seen to be most clearly defined about its middle, and to become somewhat more bulky and less sharply circumscribed in its most rostral and caudal portions.

Johnston (1915) found in the case of the turtle that the cells of the hippocampal cortex became smaller when traced caudally; this is certainly the case

in *Sphenodon*; but the striking difference in size between the cells of the hippocampus and of the general cortex mentioned by Johnston cannot be defined.

The dorso-ventral extent of the vertical portion of the hippocampus gradually decreases from before back, a feature well evidenced by comparing figs. 5 and 9 which belong to the same series and are drawn to the same scale. Rostrally it stretches almost as far ventrally as the level of the sulcus septo-striaticus (fig. 4) but, followed caudally, the ventral border is seen to recede dorsally till it coincides with the level of the sulcus fimbrio-dentatus (fig. 7). This upward recession of the hippocampal cortex coincides with the appearance and gradual increase of the septal nuclei.

The relationship of the hippocampal cortex to the general cortex will be discussed under the heading of the latter.

General cortex

In *Sphenodon* the general cortex extends from the base of the peduncle backwards over the dorsal aspect and caudal pole of the hemisphere. Medially it meets the hippocampal cortex along its whole length, whilst laterally it lies in apposition in front with the hypopallium and behind with the pyriform cortex—relationships which will be discussed more fully below.

In his account of the general cortex of *Cistudo*, Johnston (1915) figures this cell mass as coming to a somewhat tapered anterior extremity (see Johnston's fig. 7), and in the text describes how hippocampal and pyriform cortices meet rostral to the general cortex. In *Sphenodon* the general cortex certainly narrows rostrally in conformity with the diminishing size of the hemisphere, but not in so marked a manner as in *Cistudo*, and certainly no evidence of the meeting of the hippocampal and pyriform cortices is found. At the peduncular base the general and hippocampal cortices lose their identity at practically the same level; the pyriform cortex, however, continues on into the peduncle.

The general cortex possesses several distinctive features, which readily determine its identity from the hippocampal cortex. Its distinction from the pyriform cortex in cell preparations is not so striking.

As hippocampal cortex merges into general cortex the most striking change is the alteration of the texture of the whole cell mass, which gradually becomes more open. The hippocampal cortex, indeed, commences to show some evidence of this change before the general cortex is reached, and in the latter field the scattering of cells throughout the brain wall is its most characteristic feature. The scattering is chiefly towards the pia and this is most evident caudally (compare figs. 4 and 9). Despite such broadcasting of the cells, however, there may generally be detected some semblance of a column of cells running laterally from the undoubted hippocampal cortex and forming the basis of the general cortex. Nowhere does the general cortex show such a well-organised column of cells as the hippocampus; at its best it is composed

of clumps of more or less densely packed cells, welded into some semblance of a column by more scattered cells.

At its medial border the general cortex, like the hippocampus with which it is here continuous, lies about midway between the pial and ventricular surfaces, but it gradually inclines towards the ependyma and at its lateral border lies closely upon it.

Laterally the general cortex presents a feature which has been noted by Johnston (1915) in the turtle, viz. a thickening of its lateral border. This thickening is well shown in all sections of the hemisphere in *Sphenodon*, except near the rostral and caudal poles, and takes the form of a densely staining clump of cells situated at the lateral edge of the general cortex. In some measure, at least, this thickening is comparable with the feature described for *Cistudo* by Johnston, although the well-developed peripheral layer of cells described by him cannot be found in *Sphenodon*.

The lateral boundary of the general cortex in the caudal two-thirds of the hemisphere meets the pyriform cortex (figs. 6–15), while in the rostral third the general cortex turns round the dorso-lateral angle of the ventricle to become continuous with the hypopallium (figs. 1, 2, 3). Where it meets the pyriform cortex the distinction between the two, though never striking, can almost invariably be made by one means or another. Firstly may be mentioned the more densely packed clump of cells which formed the lateral boundary of the general cortex. At this point also the scattering of cells from the cortex towards the pia ceases abruptly. In the pyriform cortex itself two features which will be mentioned again below also tend to distinguish these cortical sheets; there is a tendency for the pyriform cortex to overlap the general cortex and a fairly constant flattening of the former against the ependyma. These features have been shown in many of the figures, e.g. figs. 7 and 15, where the flattening has been indicated (X).

In approximately the rostral third of the hemisphere the general cortex does not meet the pyriform cortex laterally, but passes deeply to it, close to the ependyma. It does not at once become continuous with the hypopallium, but very gradually descends as sections are traced rostrally, till ultimately it becomes continuous with the hypopallium round the dorso-lateral angle of the ventricle (fig. 3).

Examination of horizontal sections shows an interesting feature in the more rostral part of the brain wall and corresponding to the foremost portion of the general cortex. This consists in a slight, yet quite definite thickening of the brain wall wherein lies that portion of the general cortex which connects with the hypopallium. This feature is reminiscent of what occurs more strikingly in the brain of *Chelone mydas* in a similar position. Elliot Smith (1919) describes and figures the condition in that turtle, and discusses its causation on the grounds of neurobiotaxis. Certainly the appearance in *Sphenodon*, though less apparent than in *Chelone mydas*, lends support to Elliot Smith's view.

Pyriform cortex

The pyriform cortex lies along the dorso-lateral aspect of the hemisphere throughout its whole length. It extends further rostrally than the general and hippocampal cortices, and runs forwards into the peduncle. It is a better-defined sheet of cells than the general cortex, but does not present anything like the clear-cut outline of the hippocampus.

The relationship of the pyriform cortex to the general cortex on the one hand, and to the hypopallium on the other, varies as we examine sections of the brain rostrally and caudally. In the caudal two-thirds of the hemisphere the pyriform cortex is interposed between the general cortex medially and the hypopallium ventrally (figs. 5–15), whereas in the rostral third it ceases to be interposed between these two sheets and adopts a more superficial position in the brain wall. Simultaneously with this alteration in position of the pyriform cortex, the general cortex descends deep to it, and turning round the dorso-lateral angle of the ventricle becomes continuous with the hypopallium (figs. 2, 3). Rostrally, therefore, the sheet is quite cut off from the ependyma by the convergence of the general and hypopallial cortices deep to it. More caudally, where it is interposed between the general cortex and the hypopallium, it approaches the ependyma and just ventral to the general cortex lies closely in contact with it; nearer the angulus ventralis, however, it rises clear of the ependyma before bending medially to fuse with the hypopallium (fig. 8).

The transition from general cortex to pyriform cortex is marked by several features, which make the line of junction quite distinct. There is, as a rule, a tendency for the pyriform cortex to overlap the lateral border of the general cortex, and there may even be a narrow cell-free zone between them. Added to this there are definitely fewer cells scattered towards the pia over the pyriform cortex than over the general cortex, a feature which is better marked in the caudal half of the hemisphere.

The cell grouping in the pyriform cortex is also worthy of note; what would appear to be a quite constant feature is a flattening of its superficial surface just ventral to the lateral border of the general cortex, and coinciding with that part of the pyriform cortex which lies most closely upon the ependyma. This feature (marked **X** in figs. 7 and 15), moreover, is accentuated by the relative paucity of scattered cells lying superficial to it. Further ventrally, nearer the angulus dorso-lateralis, there are some cells scattered in the white matter overlying the pyriform cortex. This flattening of the pyriform cortex has been closely examined in all series, and although some do not show it in any marked degree, yet the majority confirm its presence. It may be distinguished as far rostrally as the point where the pyriform cortex commences to part company with the general cortex, and from there back to the caudal pole of the hemisphere. Its constancy is so marked that I regard it as an important feature in distinguishing this cortical sheet in *Sphenodon*.

Running ventrally from the edge of the pyriform cortex along practically its whole length there may be distinguished a layer of cells lying parallel with the pia. From their arrangement, obviously interposed in the course of the lateral olfactory tract, these cells will constitute the nucleus of that tract. Cairney (1926) has described and figured such a nucleus.

The presence of surface fissures indicating the limits of the pyriform cortex has been sought for in all series. No evidence of a rhinal fissure can be found, though the endorhinal fissure, bounding the cortical sheet ventrally, is constantly present. At this site the branches of the lateral striate artery enter the hemisphere (figs. 6, 8, 10).

The septum

The ventro-medial segment of the forebrain of *Sphenodon* presents several clearly defined nuclear masses which are, however, rather difficult to compare with the masses occupying this region in other forms. Both Hines (1923) and Cairney (1926 *b*) have given some account of the cell masses in *Sphenodon* and their descriptions have certainly proved invaluable in this study; yet in view of the material now at my disposal I consider that a more detailed and somewhat different account of this region may be given.

The term septum is here applied to that portion of the ventro-medial segment of the brain wall which lies related to the ventral extremity of the hippocampal cortex throughout the extent of the hemisphere, excluding, however, that portion of the olfacto-striatum (nucleus accumbens) which lies medial to the angulus ventralis. This arrangement has been adopted purposely by Cairney (1926 *b*), for the nucleus accumbens is evidently of the same nature as that portion of the olfacto-striatum lying lateral to the angulus ventralis, and its separation from the septum would, therefore, seem reasonable.

Thus defined, the septum will be described in two parts, rostral and caudal, owing to the fact that division into separate nuclear masses varies in these two regions.

Detailed accounts of this region in the turtle and the alligator have been given by Johnston (1915) and Crosby (1917), but the correlation of my findings with the descriptions and figures published by them is by no means easy. *Sphenodon* presents a septum in which certain clearly definable masses are present, and my aim here is to describe them accurately rather than to attempt to unravel their homologies.

In the most rostral part of the hemisphere the septum is represented by a small mass of scattered cells lying between, and quite distinct from, the olfacto-striatum ventrally and the hippocampal cortex dorsally (fig. 1). These cells are of small size and stretch from pia to ependyma. Their distinction from the olfacto-striatum is effected by a relatively cell-free zone between the two masses, but perhaps more obviously by the very different texture of the olfacto-striatum. The latter cell mass is fairly densely packed and its cells, which stain deeply, are aggregated into small clumps, whereas in the septum

the cells are discrete, small, and do not take the stain so deeply. This appearance is seen in figs. 1–5 (*n. sep. med.*). The gradually increasing proportions of the mass may be noted as traced caudally.

This first and rostral component of *Sphenodon's* septum, which I have labelled the *nucleus septi medialis*, has to this stage been unaccompanied by any other septal nucleus; but now as we proceed further caudally it comes to be separated from contiguity with the hippocampus by the advent of a second component, which appears quite suddenly (fig. 6), forming a projection into the ventricle. The cells occupying this thickening of the brain wall (the *nucleus septi lateralis*) are at first relatively few, but their large size is distinctive. At their first appearance they lie lateral to the vertical portion of the hippocampus, but when traced caudally the ventral edge of the latter recedes dorsally and, as it were, makes room for this new septal component.

The cells of the lateral septal nucleus, always distinctively large, become more and more numerous and adopt a whorled arrangement about a relatively acellular zone. This appearance is due to the fibres of the alveus system forming a bundle, which runs caudally to reach the anterior pallial commissure (figs. 7–9). The large-celled component is confined chiefly to the area lateral to the fibre bundle, and the medial small-celled septal nucleus, which lies in the main ventral to the large-celled mass, tends also to spread up the pial surface medial to the latter nucleus and the fibre bundle.

In naming the intra-ventricular sulci I have adopted the usage of Cairney (1926 *b*). The sulcus septo-striaticus is evident in all the more rostral sections, though it fades and is finally indistinguishable as the foramen of Monro is approached. It lies, I find, not strictly between the septum and the olfacto-striatum, but rather opposite the small-celled portion of the septum, a fact which might indeed justify a more accurate renaming of this sulcus in *Sphenodon* (figs. 4–7).

The sulcus fimbrio-dentatus appears suddenly like the bulge of the brain wall below it, due to the large-celled component of the septum (fig. 6). This bulge, though not projecting far into the ventricle, has a considerable dorso-ventral extent which, indeed, does not greatly vary throughout its length.

The above then represents the rostral part of the septum, clearly distinguishable by cell size and cell arrangement into its component parts and from adjacent cell masses. Caudal to this level there tends to be some merging of adjacent masses and a consequent lack of definition in their boundaries. Yet the large- and small-celled parts are distinguishable well caudally, almost to the foramen of Monro.

References in the literature to the nuclei of this region are numerous, Crosby (1917), Hines (1923), Johnston (1913 and 1915), Herrick, and Cairney (1926) have all of more recent years dealt with the subject. Hines, who treated of *Sphenodon*, did not distinguish with any degree of certainty the presence of lateral and medial septal nuclei in the adult; their presence in foetal *Sphenodon*, however, she stresses. From the foetal material at my

disposal which, however, I admit is not so early as that used by her, I fail to see any evidence of better development of these nuclei in the foetus than in the adult. Cairney was unable to find evidence either from cell characters or from cell-free zones of the presence of medial and lateral septal nuclei in the adult. In describing a small-celled medial (and ventral) nucleus and a large-celled lateral (and dorsal) nucleus I, therefore, find myself in disagreement with these two writers regarding the condition in the adult brain. The appearances I have described and figured are constantly evident in all the cell preparations studied.

Concerning the condition of this region in other forms it would appear that my lateral or large-celled nucleus corresponds in some measure, at least, to the nucleus parolfactorius lateralis in *Alligator mississippiensis* (Crosby, 1917) and to the similarly named nucleus in *Cistudo carolina* (Johnston, 1915). The rostral part of my small-celled nucleus bears a very definite resemblance to a portion of the primordium hippocampi of *Alligator* and *Cistudo*; but, apart from such resemblances, the grouping of cells in these forms is very evidently different, and a correlation of the various masses would involve further evidence than is afforded by a study of cell preparations alone. In *Chrysemys marginata* Herrick (1910) figures a lateral septal nucleus which would appear to correspond with mine.

As the foramen of Monro is approached, the clear distinctions which were evident more rostrally cannot be found; the sulcus septo-striaticus is lost, no clear distinction exists between olfacto-striatum and septum, and within the septum itself one can no longer distinguish with such ease the large-celled from the small-celled nucleus. Further specialisations also appear.

The nucleus of the diagonal band (figs. 9, 10, 11) appears just rostral to the anterior and the anterior pallial commissures and lies ventro-medially in the septum. The cells of this nucleus, which are interposed in the course of the diagonal band, are more densely packed than the cells elsewhere in the septum. Medially it lies close to the pia, whilst laterally it is related to the medial forebrain bundle. Placed as it is, in close relation to the commissures, this nucleus is moulded by them so as to present a caudal concavity which lodges them. At its caudal extremity the nucleus of the diagonal band is related to the nucleus preopticus (fig. 11), whilst ventrally some of its cells sweep laterally and ventrally round the basal aspect of the hemisphere ventral to the medial forebrain bundle. This latter feature is not so well marked in *Sphenodon* as Johnston (1915) figures it for *Cistudo*. He also considers the cells of this nucleus to be amongst the smallest in the forebrain of that turtle, but this is not so in *Sphenodon*.

There remain now the supra- and post-foraminal regions of the septum. The cells of the pre-foraminal part of the septum continue back over the foramen but, as the nucleus of the posterior pallial commissure appears and increases in size, they soon come to form an insignificant portion of the pars fimbrialis septi. This latter nucleus consists of densely packed small cells

massed round the ventro-lateral aspect of the fibre bundle running towards the posterior pallial commissure (figs. 11, 12). The caudal limit of the nucleus coincides with the sudden thinning of the hemisphere wall shown in fig. 13.

Accompanying the commissures across the mid-line are cells, which may be considered as uniting the septa of the two sides. Such cells are, however, not numerous.

The strio-amygdaloid complex

The strio-amygdaloid complex comprises, in general, the ventro-lateral segment of the hemisphere and, in a section such as that depicted in fig. 6, forms a very considerable portion of the whole brain. Dorsally it projects into the ventricle to form what Elliot Smith (1919) has called the hypopallial eminence, and Johnston (1915) the dorsal ventricular ridge. Ventrally this segment comes to the surface of the hemisphere, and stretches from the endorhinal fissure laterally to the region of the septum on the medial aspect.

The hypopallial eminence is an elongated, somewhat fusiform swelling, of greatest proportions about its middle and tapering towards its extremities. It is bounded dorso-laterally and ventro-medially by ventricular sulci to which Cairney (1926 *b*) gave the names angulus dorso-lateralis and infra-hypopallial sulcus (fig. 8). Of these, the latter does not extend the whole length of the hypopallial eminence, but falls short both rostrally and caudally (figs. 5, 12). Certain variable ventricular sulci may disturb the contour of the hypopallial eminence, and one such sulcus is seen on the dorsal aspect of the eminence in figs. 4 and 5. There is, however, on the medial aspect a constant depression shown, for example, in fig. 6; this sulcus has been noted and figured by Elliot Smith (1919). Cairney (1926 *b*) considered that this depression might lodge the projecting portion of the septum on the opposite wall of the ventricle.

The whole strio-amygdaloid complex in *Sphenodon* is not so clearly divisible into separate cell masses as in either the turtle (Johnston, 1915) or the alligator (Crosby, 1917). Certain nuclear masses are, however, definable, and to these a brief reference will be made before giving the detailed description.

Dorsally and medially, i.e. on the ventricular aspect of the hypopallial eminence, the complex is roofed by a cortex-like layer of cells, named by Elliot Smith the hypopallium. This is clearly seen, for example, in fig. 6, where it is separated from the underlying cell mass by a cell-free zone. The main mass of the complex, i.e. the palaeostriatum, presents a fairly homogeneous texture in sections such as those depicted in figs. 6 and 7. Adopting the usage of Herrick (1926), that portion lying ventrally about the angulus ventralis will be described as olfacto-striatum, and the portion passing up towards the hypopallial eminence as the somatic striatum. Cairney (1926 *b*) was unable from the cell preparations at his disposal to draw any hard and fast line between these two areas, but he considered from his study of fibre preparations that they could fairly be described separately in *Sphenodon*. In the material at

my disposal, certain additional features are evident, and from cell preparations alone it is possible to separate the two nuclei.

Under the heading, palaeostriatal cortex, will be mentioned certain nuclear masses which form a ventro-lateral cortical cap to the palaeostriatum. The two chief masses so related are the tuberculum olfactorium and the nucleus of the lateral olfactory tract (fig. 5). In the caudal part of the hemisphere the nucleus of the diagonal band and the amygdaloid nuclei also bear a similar relationship, as shown in figs. 10 and 15.

The two amygdaloid nuclei lie in the caudal pole of the hemisphere. The anterior one is of considerable size, and is placed immediately lateral to the forebrain bundles (fig. 12). The medial nucleus, much less well defined, lies lateral to the temporal horn of the ventricle, and dorso-medial to the anterior nucleus (fig. 12).

The branches of the lateral striate artery bear a quite striking relationship to the cell masses in this region, a feature which has been pointed out by Elliot Smith (1919). Throughout the major portion of the hemisphere, these vessels enter the brain at the endorhinal fissure, which is generally quite recognisable, and run dorsally and medially, sharply marking off the somatic striatum from the acellular zone immediately underlying the hypopallium (fig. 8). Towards the poles of the hemisphere this arrangement is not seen, for rostrally the branches are not in evidence at all, while caudally they run, not dorsal to the somatic striatum, but quite definitely through its midst (fig. 10). In these two regions also the somatic striatum has lost its clearly defined dorsal border, and become more diffuse; it would certainly appear, therefore, that these arteries have some influence on cell grouping in the intervening portion of the hemisphere. The various components of the strio-amygdaloid complex may now be discussed in a little more detail.

Hypopallium

This cortex-like sheet is, at the present day, being considered in two parts; an anterior part whose dominant feature is its relationship with the general cortex, and a posterior part more intimately concerned with the pyriform cortex and the amygdala. The fissure which divides these parts in some forms (fissura neo-archistriatica of Kappers, 1921) is not evident in *Sphenodon*, but the connection of the posterior part with the pyriform cortex and of the anterior part with the general cortex, which has been previously noted in *Sphenodon*, is very evident in all my series, and has been referred to above in the descriptions of the individual cortical areas. Those who have concerned themselves primarily with fibre connections, e.g. Dart (1920) and Cairney (1926 *b*), agree to such a division, and Herrick (1926) presents the same view. Dart's nomenclature will, therefore, be adopted for these two divisions of the hypopallium, viz. hypopallium anterius and hypopallium posterius.

Apart from the relationship of the hypopallium to the cortical fields, there is no precise line of demarcation between hypopallium anterius and hypo-

pallium posterius but, in the more rostral and caudal parts of the hemisphere, quite clear differences in cell arrangement can be distinguished (compare figs. 3 and 12).

The whole hypopallium may be considered as forming in transverse section a somewhat L-shaped sheet of cells, with one limb lying horizontally and meeting a cortical field laterally, and the other placed more or less vertically (fig. 5). The horizontal limb is a better-defined layer than the vertical, but together they form throughout the major portion of the hemisphere a distinctly more compact column of cells than does either the general or the pyriform cortex. This generalisation does not hold, however, at the rostral and caudal limits of the sheet.

The cells comprising the hypopallium are, if anything, slightly smaller than those of the cortical fields.

The hypopallium anterius shows its typical appearance in fig. 3 where laterally, round the angulus dorso-lateralis, it becomes continuous with the general cortex. The horizontal part is separated from the ependyma by a slight interval, and scattering of cells from it is negligible; the vertical part, on the contrary, generally lies closely apposed to the ependyma, and scattering of cells is quite obvious as well as some fragmentation of the whole column. The ventral extremity of the vertical column is rather diffuse and ill defined.

This appearance persists throughout the anterior part of the hemisphere till the region of the peduncular base is reached. Here the hypopallium rapidly diminishes (figs. 1 and 2), and the vertical column becomes more fragmented and further removed from the ependyma until the whole hypopallium anterius is represented by an irregular mass of cells arranged in several clumps.

The hypopallium posterius in its rostral part presents features identical with those described for the adjacent region of the hypopallium anterius, except, of course, that laterally it meets the pyriform cortex round the angulus dorso-lateralis. When traced caudally, fragmentation of the sheet of cells appears and gradually increases. This change is first evident in the vertical portion, but ultimately the whole mass consists of more or less isolated clumps of cells (figs. 10–12). With the appearance of the infra-hypopallial sulcus the vertical portion is given a somewhat C-shaped outline in transverse section (figs. 6–9) and its ventral extremity constantly ends at the deepest part of the sulcus. The hypopallium posterius is further removed from the ependyma than the hypopallium anterius, and the interval gradually increases as sections are traced caudally. In the most caudal, as in the most rostral sections the whole hypopallial sheet, both horizontal and vertical portions, is massed into one irregular clump (fig. 13).

The palaeostriatum

The palaeostriatum forms a large and distinctive mass of cells almost completely occupying the ventro-lateral portion of the hemisphere (fig. 6). Medially it extends round the angulus ventralis to abut on the septum;

dorsally it is in general separated from the hypopallium by a cell-free zone and by branches of the lateral striate artery; ventrally and laterally it reaches the pia. It retains connection with the pyriform cortex by means of the nucleus of the lateral olfactory tract. These features are shown in figs. 5 and 6.

In other forms cell size and grouping have been of much assistance in determining the subdivision of this area into separate nuclear masses; but in *Sphenodon* no such clear subdivision exists as is figured, for example, in the brains of the alligator (Crosby, 1917) and the turtle (Johnston, 1915). Indeed Dart (1920) considers that the alligator and the turtle exhibit unusual features of the striatal complex; I at least can agree that these forms are vastly different from *Sphenodon* in the arrangement of the cell masses, different probably in the degree of differentiation.

The following constituent parts of the palaeostriatum will now be described in more detail: palaeostriatal cortex, olfacto-striatum, somatic striatum, and the amygdaloid nuclei.

1. *The palaeostriatal cortex.* Dart (1920) has insisted on the presence in vertebrates of a cortical covering to the palaeostriatum, a covering which in reptiles, however, may be inconspicuous. In *Sphenodon* this palaeostriatal cortex is sufficiently obvious to warrant description apart from the rest of the palaeostriatum. Only in certain places do the various nuclear masses, of which it is composed, give an impression of a continuous cortical sheet.

The tuberculum olfactorium is shown in fig. 4 as a distinct layer of cells overlying the olfacto-striatum. The cells tend to be aggregated into clumps, and their staining with toluidin blue is slightly deeper than that of other parts of the palaeostriatum. Laterally the tuberculum extends out, never far removed from the pia, to meet the nucleus of the lateral olfactory tract, these two forming a quite definite cortical sheet (fig. 5). Immediately deep to this layer there is a relatively cell-free zone which further accentuates the isolation of the cortex. The cells of the nucleus of the lateral olfactory tract from their disposition are obviously lying in the midst of a fibre tract running parallel with the pia. They do not present the distinctively clumped appearance of the tuberculum, nor are they so large. Just ventral to the level of the lateral striate artery the nucleus of the lateral olfactory tract presents an enlargement (fig. 5) which is reminiscent of a similar enlargement figured by Crosby (1917) for the alligator. Dorsally the nucleus of the lateral olfactory tract is continuous with the pyriform cortex.

Further caudally the continuity of the tuberculum olfactorium and the nucleus of the lateral olfactory tract is not evident, although both are individually still quite recognisable for some distance (fig. 9). Gradually, however, both become less well organised, the tuberculum being indistinguishable from the olfacto-striatum, and the nucleus of the lateral olfactory tract failing to extend as a distinguishable entity further ventrally than the endorhinal fissure. Caudal to the level of the foramen of Monro the latter nucleus cannot be distinguished with any degree of certainty.

At a still more caudal level the nucleus of the diagonal band has a superficial relationship to the olfacto-striatum (fig. 10), and further towards the caudal pole of the hemisphere the two amygdaloid nuclei (*vide infra*) are, to some extent, disposed superficially to the somatic striatum (fig. 12).

2. *The olfacto-striatum* is most distinctive in its rostral part, fig. 5 showing a typical appearance. It is arranged about the angulus ventralis, and is capped ventrally by the tuberculum olfactorium. Its cells are massed most densely towards the ependyma; occasionally they show a radial arrangement outwards from the region of the angulus ventralis (figs. 7, 8). The portion lying medial to the angulus ventralis (the nucleus accumbens) is particularly well defined; it bulges into the ventricle between the sulcus septo-striaticus and the angulus ventralis, while dorsally it meets the small-celled portion of the septum.

The border-line between the nucleus accumbens and the septum is worthy of note. A definite cell-free zone is quite frequently present, separating these two areas (figs. 3, 4, 5), and the dorsal convex border of the olfacto-striatum may show a row of densely packed cells, which very clearly denotes the line of demarcation. In addition to these features the general arrangement of the cells in the two areas is quite different, those of the medial septal nucleus being small and discrete while the olfacto-striatum presents larger cells arranged in coarse clumps. This arrangement of the cells of the olfacto-striatum in coarse clumps is, perhaps, its most striking feature.

The segment of the brain wall between the sulcus septo-striaticus and the angulus ventralis is not completely occupied by this portion of the olfacto-striatum (the nucleus accumbens). As mentioned in connection with the septum the sulcus septo-striaticus does not lie exactly between the areas indicated, but rather indents the medial aspect of the small-celled (medial) septal component. Further, this portion of the olfacto-striatum is, to some extent, kept from contact with the pia, on the one hand by a prolongation downwards of the septal cells, and on the other hand by a tendency for the tuberculum olfactorium to spread upwards (fig. 8).

That portion of the olfacto-striatum lying lateral to the angulus ventralis is very similar in the rostral part of the hemisphere to the more medial portion. It is approximately of the same size, but does not present the same clear outline. The cells are a little less densely packed and are aggregated into smaller clumps (fig. 5). Its lateral border is ill-defined and reaches out in a scattered manner as far as the ventral limit of the hypopallium anterius. The nucleus of the lateral olfactory tract lies on its ventro-lateral aspect (fig. 4). In this latter figure it may also be seen to be separated from the somatic striatum by a relatively cell-free zone.

When the olfacto-striatum is examined in sections rostral to that shown in fig. 5, its medial portion is seen to persist in its typical form just medial to the angulus ventralis, whereas the lateral portion becomes less extensive. The whole mass indeed becomes more circumscribed as well as smaller. As the

angulus ventralis flattens out and disappears the olfacto-striatum also diminishes and is finally lost. It is impossible to distinguish the olfacto-striatum from the tuberculum olfactorium in the most rostral sections.

If now the olfacto-striatum is traced caudally from the level represented by fig. 4 it is seen at first to be represented by a well-defined mass both medial and lateral to the angulus ventralis. Between it and the tuberculum olfactorium there is often recognisable a more or less cell-free zone; laterally it abuts on the somatic striatum, but here there is an area where the cells are sparse, and thus a lateral boundary is denoted (fig. 5). Gradually the two masses fuse, with no suggestion of any intervening cell-free zone (fig. 6); nevertheless a distinction between them is possible, for the olfacto-striatum retains its coarsely clumped arrangement, whilst the somatic striatum, although presenting aggregations of cells, does not in general show such coarse clumps, but rather small aggregations often arranged in a linear manner. This arrangement suggests their interposition in the course of the lateral forebrain bundle as it sweeps dorsally, and is in keeping with Cairney's (1926 *b*) findings in connection with the disposition of that bundle. At a level such as that shown in fig. 6 the cell size of the two components of the palaeostriatum affords no evidence of their different nature.

Caudally from this they may again be distinguished, for the forebrain bundles, medial and lateral, are commencing to disperse the cells and divide the whole palaeostriatum into lateral and medial components (figs. 8, 9). To some extent in these two figures the olfacto-striatum may be said to possess again the features which were typical of it at a more rostral level. The lateral part tends to run along the ependyma, but cannot be said to reach the infra-hypopallial sulcus; rather the somatic striatum and the olfacto-striatum are connected here by a band of cells, but the exact boundary is quite indistinct. Nearer the pia, however, the intervention of the lateral forebrain bundle makes the boundary line more obvious.

Towards the foramen of Monro the olfacto-striatum becomes less densely packed, the clumping of cells is by no means so evident and a tuberculum olfactorium is less readily detected. The nucleus of the diagonal band (figs. 9, 10) runs round close to the pia, medial and then ventro-medial to the olfacto-striatum. In fig. 10, in the midst of the olfacto-striatum, the medial forebrain bundle is clearly identifiable, with a few cells in its midst.

3. *Somatic striatum.* This nuclear mass does not extend so far rostrally as the olfacto-striatum, so that, in figs. 2 and 3, where the latter is readily recognisable the somatic striatum is absent as a cell mass. At this level, and rostral thereto for a short distance, the interior of the hypopallial eminence is occupied by a few scattered cells from the hypopallial cortex. In fig. 4 the rostral extremity of the somatic striatum is shown rising up into the hypopallial eminence from below. It is covered ventro-laterally by the nucleus of the lateral olfactory tract. The cells here are irregularly arranged and present a few clumps; their size is not distinctive. The presence of a relatively cell-free

zone, however, between it and the olfacto-striatum enables it to be readily separated from the latter mass. The next two figures (4 and 5) show an extension dorsally which is limited above and laterally by the branches of the lateral striate artery, but which medially and below is not very clearly defined from the hypopallium and the olfacto-striatum.

With the appearance of the lateral forebrain bundle as a definite structure (fig. 8) the somatic striatum becomes chiefly confined to the dorsal part of the hypopallial eminence. The cells, which are frequently arranged in linear groups, extend over the infra-hypopallial sulcus into the overhanging portion of the hypopallial eminence. In the region of the endorhinal fissure the somatic striatum constantly extends towards the pia (figs. 7, 8, 9), and here comes into relation with the nucleus of the lateral olfactory tract.

The area occupied by the lateral forebrain bundle is relatively acellular; what cells there are, are distinguished by their large size and light staining with toluidin blue (figs. 8, 9, 10). This feature of the somatic striatum I take to have some relationship to the lateral large-celled (lenticular) nucleus in a similar position in *Cistudo* (Johnston, 1915). It is to be noted, however, that the large-celled area of *Sphenodon* is much less extensive than the similarly placed area described by Johnston. These large cells are no longer evident at the level of the foramen of Monro. The somatic striatum here is represented by relatively few cells occupying the core of the hypopallial eminence (fig. 11).

4. *Amygdaloid nuclei.* Two amygdaloid nuclei are distinguished in *Sphenodon* and, following the nomenclature chosen by Cairney, they are designated nucleus anterior amygdalae which is also lateral and nucleus medialis amygdalae.

The *anterior amygdaloid nucleus* is a conspicuous mass composed of densely packed small cells. In front it commences at a level just rostral to the foramen of Monro and immediately lateral to the lateral forebrain bundle on which the nucleus is moulded. Fig. 11 shows the mass a short distance caudal to its commencement. The nucleus possesses considerable antero-posterior extent, reaching back to the caudal pole of the hemisphere. There is nothing in cell preparations to suggest any continuity of this nucleus with the cell masses forming either olfacto-striatum or somatic striatum; it arises as a new structure, independent of these elements. Its lateral extremity, pointed and straggling, would appear to have some continuity with the nucleus of the lateral olfactory tract which, however, at this caudal level is not at all well defined.

Cairney (1926 *b*) has made the statement that this nucleus in *Sphenodon* may be divisible into medial and lateral components. I cannot find any evidence from cell preparations in support of such a division. The core of the nucleus is densely packed with cells and stands out very clearly in many sections (fig. 12); but this appears to be no more than a central denser aggregation.

In the caudal pole of the hemisphere the nucleus gradually diminishes; it here becomes related medially and dorsally to the medial amygdaloid nucleus (fig. 13).

There are two extensions medially from the anterior amygdaloid nucleus, one dorsal and one ventral to the forebrain bundles. Of these two extensions the dorsal is the more caudal and also the better marked.

The ventral extension is carried medialwards beneath both forebrain bundles as an interstitial nucleus of the diagonal band of Broca. It establishes a slender connection with the better-marked, more medially placed nucleus of the diagonal band (fig. 11).

The dorsal extension (fig. 12) sweeps medially over both forebrain bundles to establish continuity with the nucleus preopticus and the nucleus periventricularis hypothalami. It may, therefore, be looked upon as the interstitial nucleus of the tractus amygdalo-preopticus and of the tractus amygdalo-hypothalamicus anterior, both of which it accompanies.

The *nucleus medialis amygdalae* is an ill-defined mass, but is characterised by being composed of cells which, while staining less densely than those of the anterior amygdaloid nucleus, are definitely larger; this is in keeping with Johnston's findings for *Cistudo*.

It comes into existence with the temporal horn of the ventricle to which it lies lateral; traced caudally its bulk increases, and its ventral extremity approximates to the medial aspect of the anterior amygdaloid nucleus which is now becoming less conspicuous (fig. 13). At its best this nucleus is not nearly so well defined as either the hypopallium dorsal to it or the anterior amygdaloid nucleus placed ventro-laterally. Its distinction from the hypopallium posterius is made by the characteristic densely staining clumps of smaller cells composing the latter.

Dart (1920) describes in *Sphenodon* two nuclei of virtually the same position as these. The nucleus anterior amygdalae of this description would correspond with Dart's nucleus tractus taenia, and the nucleus medialis amygdalae with his nucleus amygdalae proprius.

CENTRES OF THE TELENCEPHALON MEDIUM

This region contains two nuclear masses which are proper to it, viz. the nuclear preopticus and the nucleus supraopticus. There are, however, as will be seen in the diagrams mentioned below, other masses abutting on it; these latter are described with the regions to which they belong.

The nucleus preopticus

The nucleus preopticus consists of densely-packed small cells arranged about the recessus preopticus of the third ventricle (figs. 11, 12). Its rostral extremity lies on a plane just anterior to the foramen of Monro and slightly precedes the appearance of the recess itself. Caudally the mass merges with the nucleus periventricularis hypothalami.

The cells are most densely packed ventrally (fig. 11) where the mass is closely adjacent to the optic chiasma. A distinct appearance of lamination is

also evident in the ventral half of the nucleus. Huber and Crosby (1926) considered the lamination of this nucleus in the alligator to be less marked than that in the nucleus periventricularis hypothalami. I find that in *Sphenodon* the lamination is equally well marked in both nuclei (compare figs. 11 and 12).

The relationship of the nucleus to the ependyma varies; rostrally the two are closely related but, as sections are traced caudally towards the third ventricle, a gradually increasing interval exists between them. At the level of the third ventricle the interval has become quite considerable (fig. 13).

The nuclei of the diagonal bands of the two sides are immediate dorso-lateral relations in the rostral part of the nucleus, where indeed they appear to compress it. Further caudally, beyond the limits of the nucleus of the diagonal band, the nucleus preopticus becomes more diffuse at its periphery and extends further laterally to become directly related to the medial forebrain bundle (fig. 12).

A connection with the nucleus anterior amygdalae is established by means of the interstitial nucleus accompanying the tractus amygdalo-preopticus over the dorsal aspect of the forebrain bundles (fig. 12).

The nucleus supraopticus

At the level of the foramen of Monro, and lying ventro-medial to the forebrain bundles, between them and the chiasma, is found this somewhat flattened mass of cells (figs. 12, 13). They are characterised by their large size and deep staining with toluidin blue.

Fig. 12 shows the rostral extremity of the mass which does not at this level extend laterally; further caudally a few cells stretch ventral to the forebrain bundles almost as far as the lateral limit of the lateral forebrain bundle. At its medial extremity it meets the nucleus preopticus. There is a marked difference in size between the cells of these two nuclei.

Johnston (1915) has figured a similarly named nucleus in the turtle.

CENTRES OF THE DIENCEPHALON

The epithalamus

The *epithalamus* or *habenula* of *Sphenodon* forms a prominent projection on the dorsal aspect of the diencephalon. It contains two distinct nuclear masses, whose essential relationship to each other is rostral and caudal. In accordance with the nomenclature used in other forms, Cairney (1926 *b*) has named these masses the medial and lateral habenular nuclei, and he claimed as justification for so naming them the fact that the caudal nucleus overlapped the rostral to some extent on its lateral aspect.

I cannot verify all Cairney's findings and, therefore, cannot agree to his nomenclature. That there are two distinct nuclear masses is beyond dispute, rostral and caudal; moreover, the caudal nucleus is somewhat dorsal, for it overlaps the caudal extremity of the rostral nucleus. I fail to find any evidence

of the caudal nucleus lying lateral to the rostral. These masses have, therefore, been named the rostral and caudal habenular nuclei, and correspond to Cairney's medial and lateral nuclei. Dendy's (1910) habenular nucleus is undoubtedly, as Cairney notes, only the caudal (Cairney's lateral) nucleus of *Sphenodon*. There is no evidence of the greater size of the nucleus of one side as Dendy suggested.

The *rostral habenular nucleus* throughout the major portion of its extent lies just medial to the stria medullaris (fig. 14). Its ventral boundary is frequently marked by the presence of a row of densely packed cells, beneath which there is generally a quite distinguishable cell-free zone separating the habenular from the subjacent thalamic nuclear masses. This cell-free zone also extends between the ependyma and the rostral habenular nucleus—a feature in striking contrast to the intimate relationship of the caudal habenular nucleus and the ependyma (fig. 16).

Rostrally this habenular nucleus is poorly defined, scarcely making any projection on the dorsal aspect of the diencephalon. Its caudal extremity becomes related on its dorsal aspect to the caudal habenular nucleus (fig. 16). The latter nucleus at first lies rather dorso-medial than directly dorsal to the rostral nucleus. There is some fusion of the two masses where they are contiguous. The cells of the rostral nucleus are medium-sized and loosely packed. Subdivision of the mass into various components along the lines suggested by Huber and Crosby (1926) cannot be made in *Sphenodon*.

The *caudal habenular nucleus* is composed of slightly smaller cells which stain deeply with toluidin blue. It is characterised by its close association with the ependyma, from which, indeed, it often cannot be distinguished. Like the more rostrally placed nucleus it is somewhat elongated, and instead of lying medial to the stria medullaris it is invaded by it and so broken up into numerous islands, giving the whole mass a reticulated appearance (fig. 17).

Its rostral extremity appears as a densely staining mass of cells immediately subjacent to the ependyma and dorsal to the caudal extremity of the rostral nucleus. It rapidly grows as traced caudally and produces a well-marked prominence on the dorsal aspect of the diencephalon (figs. 16, 17). To this prominence the wall of the dorsal sac is attached.

At the level of the habenular commissure (fig. 18) the two nuclei of opposite sides are fused into a crescentic mass across the mid-line. They can be traced for only a short distance caudal to the habenular commissure, and retain the characteristic reticulated appearance and close association with the ependyma to their caudal extremity.

The thalamus

The detailed work of Huber and Crosby (1926) on the thalamus of the alligator has greatly facilitated the study of the cell masses in *Sphenodon*, many of the thalamic nuclei of the latter being exactly comparable with those described for the alligator.

While the major part of the thalamus of *Sphenodon* is clearly divisible into nuclei, the remainder presents a somewhat ill-defined appearance. Cairney (1926 *b*) described only those masses which were readily demonstrable in his preparations, and to the clear accounts of such nuclei as he described I have been able to add but little. A description of several other nuclei, not included in his paper, is given here. The features of the third ventricle have been sufficiently reviewed by Cairney to make any further description unnecessary.

Nucleus ovalis

This is a small clearly circumscribed mass of cells lying dorsal to the basal forebrain bundle in the caudal part of the infra-foraminal region (fig. 13). It is deeply placed, being nowhere in contact with either pia or ependyma. It is closely comparable with the similarly named mass in the alligator (Huber and Crosby, 1926).

The stria medullaris lies lateral to it, and somewhat dorsal, as it sweeps upwards. Ventrally the basal forebrain bundle is in general related, but in the rostral part of the nucleus ovalis the tractus amygdalo-hypothalamicus and its interstitial nucleus intervene between it and the basal forebrain bundle. The recessus prenuclearis bounds the mass caudally. On its medial aspect some of the most rostral cells of the nucleus dorsomedialis anterior (*v.i.*) may be detected.

The mass is, as it were, clothed by a cortex of its own cells, giving the nucleus a quite characteristic appearance in sections through all planes. The core, within this cortical covering, is composed of relatively few loosely packed cells. This appearance might be due in part at least to shrinkage, but is nevertheless sufficiently marked in all series to be quite discernible and I, therefore, consider it a feature of this cell mass.

The cells comprising the nucleus ovalis are of medium size, and take only a light stain with toluidin blue.

There may be seen in fig. 13, lying a short distance lateral and ventral to the nucleus ovalis, a few large cells. They are not apparently part of the nucleus ovalis, nor can I find any reference to a similarly placed mass in other forms. It can be traced through only a few sections, and has no obvious continuity with any other cell mass.

Nucleus dorsomedialis anterior, nucleus dorsolateralis anterior, and nucleus rotundus

These three nuclei are very closely associated and almost completely occupy the dorsal portion of the diencephalon (figs. 14, 15, 22). The nucleus rotundus lies rather caudal to the other two and is interposed between them. They lie dorsal to the plane of the recessus prenuclearis. The three masses are so closely interrelated that they may best be described together.

The whole mass may be described as being related on its dorsal aspect to the habenula, a cell-free zone intervening (fig. 16). Medially it is separated

from the ependyma by the periventricular fibre system (fig. 14), but as we shall see subsequently, the nucleus dorsomedialis anterior approximates closely in one place to the ependyma. Laterally lies the stria medullaris and the dorsal part of the lateral geniculate body (fig. 14). The recessus prenuclearis is related ventrally (figs. 14, 16).

Rostral to the level of the nucleus rotundus the dorso-medial and dorso-lateral nuclei lie closely side by side, meeting along an oblique line (figs. 14, 16, 21, 22). The cells of the former are small, fairly densely packed and stain deeply with toluidin blue, while those of the dorso-lateral nucleus are definitely larger, loosely packed and take a more hazy stain. Both masses diminish in size when traced rostrally, but identification is possible almost to the level of the foramen of Monro where some cells of the dorso-medial nucleus, which proceeds further rostrally than its companion nucleus, become related to the medial aspect of the nucleus ovalis (fig. 13). The extension of the dorso-medial nucleus rostrally beyond the dorso-lateral nucleus is shown clearly in horizontal sections (figs. 21, 22).

The interposition of the nucleus rotundus between the other masses profoundly modifies them. The nucleus rotundus is, as it were, pushed in between them from the caudal aspect, but it is the dorso-medial nucleus which is most distorted. The latter mass is largely excavated to accommodate the nucleus rotundus, and is also displaced medially against the ependyma so that no interval is discernible between them (figs. 15, 22). In this manner the nucleus dorsomedialis is divided into a peripheral thicker part and a central thin area. Horizontal sections, therefore, show more massive rostral and caudal portions united by a narrow isthmus (fig. 22); in transverse sections the isthmus unites dorsal and ventral portions of the nucleus (fig. 15). In the latter figure the dorso-medial nucleus is seen to extend across the whole ventral aspect of the nucleus rotundus, and then even somewhat dorsally, to meet the dorso-lateral nucleus. Thus the nucleus rotundus is surrounded on three aspects by the nucleus dorsomedialis anterior and retains contact with the dorso-lateral nucleus over a relatively small area.

The dorso-lateral nucleus is of considerably less rostro-caudal extent than the other two masses under discussion, being related to little more than the rostral half of the nucleus rotundus. In horizontal sections it presents a well-defined caudal extremity and an oblique surface towards the nucleus rotundus (fig. 22).

The caudal extremities of the nucleus rotundus and the nucleus dorso-medialis anterior are ill-defined but are, in general, related to the nucleus lentiformis thalami (fig. 22). Ventrally and caudally the dorsal peduncle of the basal forebrain bundle sweeps up towards the nucleus rotundus and the nucleus dorsolateralis anterior, which in this region are therefore somewhat irregular and relatively acellular (figs. 17, 22).

The main features of the nucleus rotundus have already been covered in the description of the dorso-medial and dorso-lateral nuclei. Its cells are

intermediate in size between those of the two masses between which it is interposed, and are not packed so densely as those in the dorso-medial nucleus. In horizontal sections it presents an elongated outline, a very well-defined rostral extremity, but a rather irregular caudal one due to the entrance of fibre bundles from the dorsal peduncle (fig. 22). Cairney has clearly figured the arrangement of these fibres relative to this mass.

Some cells of the nucleus rotundus extend caudally ventral to the recessus geniculi. In this region (figs. 19, 20) the nucleus rotundus is a rather indefinite mass, and has lost the clear outline which characterised it more rostrally. It is interposed between the nucleus periventricularis hypothalami medially and the nucleus lentiformis thalami laterally.

Corpus geniculatum laterale

This elongated mass has had its position in the thalamus clearly defined by Cairney (1926 *b*), who has also stated its fibre connections. On examination of many series the most striking attribute of the whole mass is the very marked difference in its definition in fibre and in cell preparations. In Weigert sections, such as Cairney figures in his paper, the lateral geniculate body is indeed well-defined and readily divisible into its two components, dorsal and ventral. A study of cell preparations, however, shows a much less convincing picture, although certainly the same two elements may be detected.

As seen in fig. 14 the mass lies lateral to the nucleus dorsolateralis anterior and to the area triangularis, and has the optic tract lying superficially.

The dorsal component, which is connected with only the rostral part of the ventral component, is directly caudal to the nucleus ovalis and is loosely packed with cells (figs. 14, 15). Medially the cells are condensed into a compact layer, where staining with toluidin blue is deeper. This aspect abuts directly upon the nucleus dorsolateralis anterior (fig. 22). Huber and Crosby (1926) have noted this deeply staining layer in the alligator. In *Sphenodon* it is very closely associated with the laminations of the area triangularis (*v.i.*) and will again be mentioned in that connection. The area triangularis forms a conspicuous medial relation of the lateral geniculate body, particularly of its dorsal component, and separation of the two masses is not distinct (figs. 14, 15, 16). The cells of the lateral geniculate body are slightly larger than those of the area triangularis.

The ventral portion of the lateral geniculate body is considerably more elongated than the dorsal but much less distinct in cell preparations; there is a notable paucity of cells (figs. 14, 15, 16). It also lacks the condensed medial layer and has not the same continuity with the area triangularis. Cairney found in some sections evidence of a medial condensation of cells in the ventral part of the lateral geniculate body. I find such a condensation to be confined to the dorsal component.

Area ventralis anterior and area triangularis

These names are taken from Huber and Crosby's paper (1926) on the alligator to describe what would appear to be a homologous cell mass in *Sphenodon*.

The area ventralis anterior may readily be picked up just ventral to the recessus prenuclearis, where it forms a well-defined wedge-shaped mass with the apex related medially to the nucleus periventricularis hypothalami and its scattered base laterally to the lateral geniculate body (fig. 14). This portion of the area ventralis anterior is so distinctive that Huber and Crosby have specially named it the area triangularis. Here there is a very definite lamination of the cells round the lateral aspect of the recessus prenuclearis; some of this mass is in apparent continuity with the medial compact portion of the lateral geniculate body. The relationship of the area triangularis to the lateral geniculate body is just as intimate in *Sphenodon* as Huber and Crosby have figured for the alligator.

The mass extends for some distance rostral to the level of the recessus prenuclearis, lying ventral to the nucleus dorsolateralis anterior, and still further rostrally it becomes related to the nucleus ovalis. This rostral portion is a poorly organised mass of cells, but is recognisable in all series.

Caudal to the recessus preopticus the area ventralis remains for a space as a definite laminated mass, but ultimately becomes indistinguishable from the nucleus entopeduncularis.

The mass is related ventrally to the basal forebrain bundle, and in its caudal part it adopts a curved outline in conformity with it (fig. 16).

Nucleus entopeduncularis

Huber and Crosby (1926) have described an ento-peduncular nucleus occurring in the midst of the lateral forebrain bundle in the thalamus. The mass here described lies amongst the fibre bundles of the dorsal peduncle of the basal forebrain bundle. It is evident in figs. 14, 15, 16 and 17. It consists of scattered groups of cells, mostly of medium size, but with an admixture of larger cells. In cell preparations this discrete arrangement of cells in an otherwise cell-free zone serves to distinguish the dorsal from the ventral peduncle, for the latter is practically acellular.

Nucleus lentiformis thalami

This nucleus, lying caudally in the thalamus, is related chiefly to the recessus geniculi of the third ventricle but extends for some distance rostral to this level (figs. 19, 20). It slopes ventrally from before back so that in a horizontal section such as fig. 22 only the caudal part of the nucleus is shown. It lies dorso-lateral to the nucleus rotundus, forming a sloping roof-like expansion over the caudal portion of this mass (figs. 19, 20) separating it from the more

dorsally placed habenula and from the posterior commissure. The tractus habenulo-peduncularis runs between the nucleus rotundus and the nucleus lentiformis and is evident in cell preparations as a clear zone. The nucleus is best defined at the level of the recessus geniculi (fig. 20), where it extends round the lateral aspect of the recessus to lie for a short distance ventral to its blind extremity where it becomes related to the nucleus rotundus. In this region the cells are more densely packed and present some lamination.

Rostrally the mass is merely a scattered row of cells extending laterally and ventrally from the region of the organon subcommissurale. The cells in this rostral part are most densely packed laterally, and form medially a loose straggling column which is closely related above to the organon.

The cells of the nucleus lentiformis are not of uniform size. There is a well-defined zone of distinctly larger cells lying in that portion of the nucleus just dorsal to the extremity of the recessus geniculi. This mass of larger cells is not marked off in any way from the general contour of the nucleus lentiformis, but is nevertheless a distinct feature in all series examined.

It is difficult to find any resemblance between this mass and the nucleus posterocentralis of Huber and Crosby (1926), which they suggest might be homologous with the nucleus lentiformis of Kappers. The latter writer (1921) figures a nucleus lentiformis thalami in sagittal section, which corresponds to the mass described here both in position and in its relations to other masses.

THE HYPOTHALAMUS

The hypothalamus of *Sphenodon* is not differentiated into separate nuclei to such an extent as Huber and Crosby (1926) have described for the alligator. Apart from the well-marked nucleus periventricularis hypothalami it presents no clearly defined nuclear masses.

The *nucleus periventricularis hypothalami* surrounds the ventral part of the third ventricle. Rostrally it is continuous with the nucleus preopticus, and caudally comes into relationship with the cells of the tectum opticum. The nuclei of the two sides form a somewhat U-shaped mass (fig. 14) which is, as a rule, most densely packed with cells ventrally. Some degree of lamination of its cells may generally be seen.

There is a definite interval separating this nucleus from the ependyma, and this interval is occupied by the peri-ventricular fibre system. The interval is widest dorsally, and a few large cells are constantly found here at the level of the recessus prenuclearis (figs. 14, 16).

The dorsal extremity of the nucleus varies in different regions. Rostrally it receives the tractus amygdalo-hypothalamicus anterior and its interstitial nucleus which have crossed dorsal to the forebrain bundles. Some part of this interstitial nucleus may be seen in fig. 13. At the level of the recessus prenuclearis the dorsal extremity of the peri-ventricular nucleus sweeps laterally, ventral to the recess and gains contact with the area triangularis (figs. 14, 16),

but is apparently not continuous with it, for the cells of the latter tend to end abruptly at its medial extremity, a feature clearly indicated in fig. 16.

Caudal to the level of the recessus prenuclearis the dorsal border of the peri-ventricular nucleus extends further dorsally, and becomes related to the caudal and ventral aspects of the nucleus rotundus and the nucleus dorso-medialis anterior (figs. 15, 19, 20).

In fig. 15, and in sections adjacent to it, the dorsal extremity of the peri-ventricular nucleus may be seen to end in a somewhat enlarged mass of cells which lies ventro-medial to the nucleus rotundus, but separated from it by an extension of the nucleus dorsomedialis anterior. The cells forming this mass are larger than those of the main portion of the peri-ventricular nucleus, further ventrally with which it is connected by some much smaller cells. That this mass forms a portion of the peri-ventricular nucleus I am not at all certain. It bears some resemblance to the area ventromedialis of the alligator (Huber and Crosby, 1926), and may quite possibly be the corresponding mass. Their area ventromedialis is also connected to the nucleus periventricularis hypothalami by a microcellular nucleus.

The lateral border of the nucleus periventricularis is indefinite; cells scatter laterally into the adjacent white matter, becoming more and more sparse towards the pia. Dorsally it is related to the area triangularis, the nucleus entopeduncularis (fig. 14) and to the basal forebrain bundle. The latter bundle, to some extent, determines the contour of the lateral aspect of the peri-ventricular nucleus (figs. 19, 20).

Amongst the cells extending laterally from this nucleus towards the pia there are no identifiable nuclear masses such as Huber and Crosby (1926) have described in the alligator.

SUMMARY

1. The cerebral cortex is composed of three clearly definable sheets, a medial hippocampal cortex, a lateral pyriform cortex, and between these the general cortex. Attention is drawn to the densely staining clump of cells which as a rule forms the lateral boundary of the general cortex. The pyriform cortex presents laterally a flattened area of marked constancy but of obscure causation. The relationship of pyriform cortex laterally to the hypopallium varies; caudally the two sheets meet at the angulus dorso-lateralis while rostrally the pyriform cortex lies superficially in the brain wall, and is separated from the ependyma by the meeting of the general cortex and the hypopallium. The brain wall shows some increase in thickness where the general cortex and the hypopallium meet.

2. The septum shows, in its pre-foraminal part, two distinct nuclear masses which have been termed nucleus septi medialis (which is also ventral) and nucleus septi lateralis (also dorsal). The lateral nucleus does not extend so far rostrally as the medial and is composed of distinctively large cells. The

sulcus septo-striaticus is claimed to lie not opposite the interval between the septum dorsally and the olfacto-striatum ventrally, but rather opposite the medial small-celled septal nucleus. Caudally in the septum other specialised masses are described, viz. the nucleus of the diagonal band and the nucleus of the posterior pallial commissure.

3. The ventro-lateral segment of the hemisphere in *Sphenodon* is not at all similar in the appearance of its cell masses to such forms as the alligator and the turtle. The hypopallium is divisible into anterior and posterior parts, the former meeting the general cortex laterally and the latter the pyriform cortex. There is no sharp line of demarcation between these two components of the hypopallium within the cell mass itself, but towards the poles of the hemisphere they present quite different appearances due to dissimilar cell grouping.

The somatic striatum and olfacto-striatum are related to the lateral and medial forebrain bundles respectively. Their distinction in cell preparations depends almost entirely on differences in cell grouping, variations in cell size being of little assistance.

A palaeostriatal cortex has been described consisting of those nuclear masses which are arranged about the ventro-lateral aspect of the palaeostriatum as a cortical covering; the tuberculum olfactorium and the nucleus of the lateral olfactory tract are the chief masses so related, though towards the caudal pole of the hemisphere the nucleus of the diagonal band and the amygdaloid nuclei have a somewhat similar relationship to the palaeostriatum.

4. Two habenular nuclei are described and named rostral and caudal. These appear without any doubt to correspond to the medial and lateral nuclei of other forms, but I fail to detect any evidence of a medio-lateral relationship between them.

5. The individual descriptions of the cell masses in the thalamus and hypothalamus are not lengthy and will not, therefore, be discussed to any extent here. The majority of them are well-defined, circumscribed masses, readily lending themselves to reproduction in the figures. Some others, less definite in form and in significance, have been tentatively discussed. In connection with these latter masses the work of Huber and Crosby (1926) on the alligator has been found most useful.

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EXPLANATION OF FIGURES

The figures accompanying this paper, with the exception of the last two, represent in the order of their numbers a series of transverse sections through the forebrain from before back. Figs. 1 to 13 and 16 to 18 are drawn from sections of the same brain (G.B. 82); likewise figs. 14, 15, 19 and 20 (G.B. 64). The last two figures, 21 and 22, show horizontal sections through the thalamus (G.B. 85).

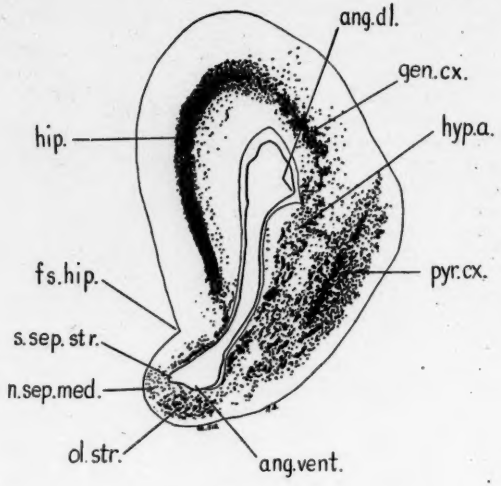
Frequent reference to the figures has been made throughout the text where an indication of the level of the section is also frequently given. For this reason legends have not been attached.

All figures have been drawn to the same degree of magnification by projection of the actual sections. Cell size is not strictly to scale, but variation in the size of cells has been indicated.

ABBREVIATIONS USED IN FIGURES

a.triang.	Area triangularis.
ang.dl.	Angulus dorsolateralis.
ang.vent.	Angulus ventralis.
art.	Branch of the lateral striate artery.
b.f.b.	Basal forebrain bundle.

c.gen.l.d.	Corpus geniculatum laterale, pars dorsalis.
c.gen.l.v.	Corpus geniculatum laterale, pars ventralis.
ch.	Optic chiasma.
com.ant.	Commissura anterior.
com.hab.	Commissura habenularum.
com.pal.ant.	Commissura pallii anterior.
com.pal.post.	Commissura pallii posterior.
f.	Foramen of Monro.
fs.hip.	Fissura hippocampi.
gen.cx.	General cortex.
hip.	Hippocampus.
hyp.a.	Hypopallium anterius.
hyp.p.	Hypopallium posterius.
l.f.b.	Lateral forebrain bundle.
m.f.b.	Medial forebrain bundle.
n.ant.amyg.	Nucleus anterior amygdalae.
n.com.p.p.	Nucleus commissurae pallii posterioris.
n.d.b.	Nucleus of the diagonal band.
n.dl.a.	Nucleus dorsolateralis anterior.
n.dm.a.	Nucleus dorsomedialis anterior.
n.entop.	Nucleus entopeduncularis.
n.hab.c.	Caudal habenular nucleus.
n.hab.r.	Rostral habenular nucleus.
n.int.	Interstitial nucleus of tractus amygdalo-preopticus and of tractus amygdalo-hypothalamicus anterior.
n.lent.th.	Nucleus lentiformis thalami.
n.med.amyg.	Nucleus medialis amygdalae.
n.oval.	Nucleus ovalis.
n.periv.hyth.	Nucleus periventricularis hypothalami.
n.preop.	Nucleus preopticus.
n.rot.	Nucleus rotundus.
n.sep.lat.	Nucleus septi lateralis.
n.sep.med.	Nucleus septi medialis.
n.supraop.	Nucleus supraopticus.
n.tr.olf.lat.	Nucleus tractus olfactorii lateralis.
org.sc.	Organon subcommissurale.
ol.str.	Olfacto-striatum.
pyr.cx.	Pyriform cortex.
rec.gen.	Recessus geniculi.
rec.preop.	Recessus preopticus.
s.endor.	Fissura endorhinalis.
s.f.d.	Sulcus fimbrio-dentatus.
s.inf.hyp.	Sulcus infrahypopallialis.
som.str.	Somatic striatum.
s.sep.str.	Sulcus septo-striaticus.
temp.horn.	Temporal horn of the lateral ventricle.
tub.olf.	Tuberculum olfactorium.
w.d.s.	Wall of dorsal sac.
x.	Flattening of pyriform cortex referred to in text.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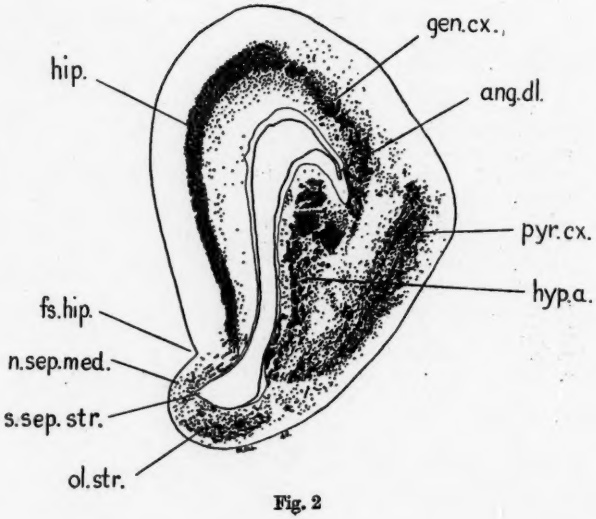
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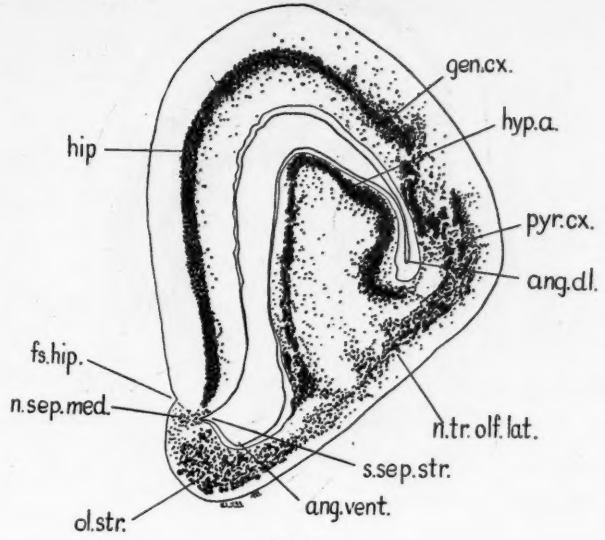
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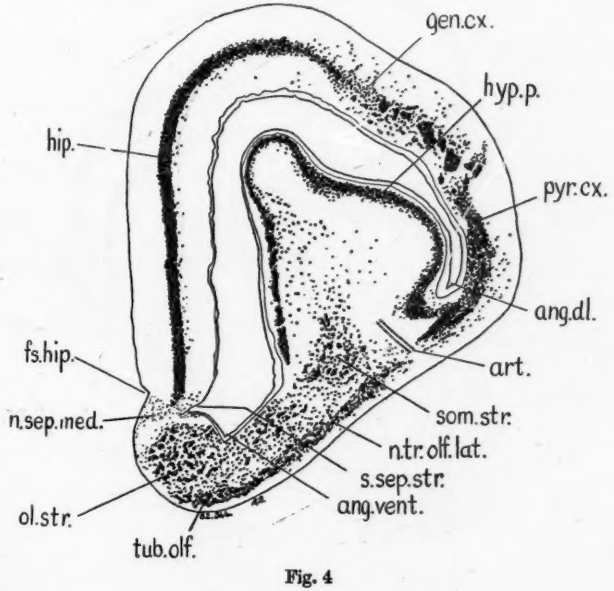
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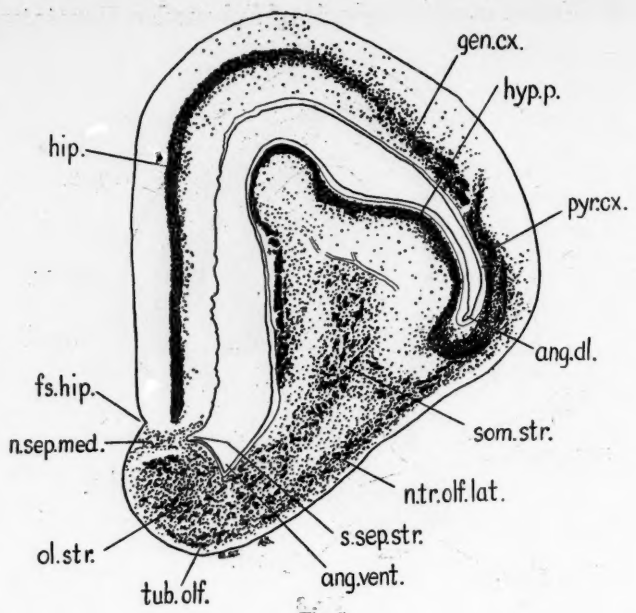
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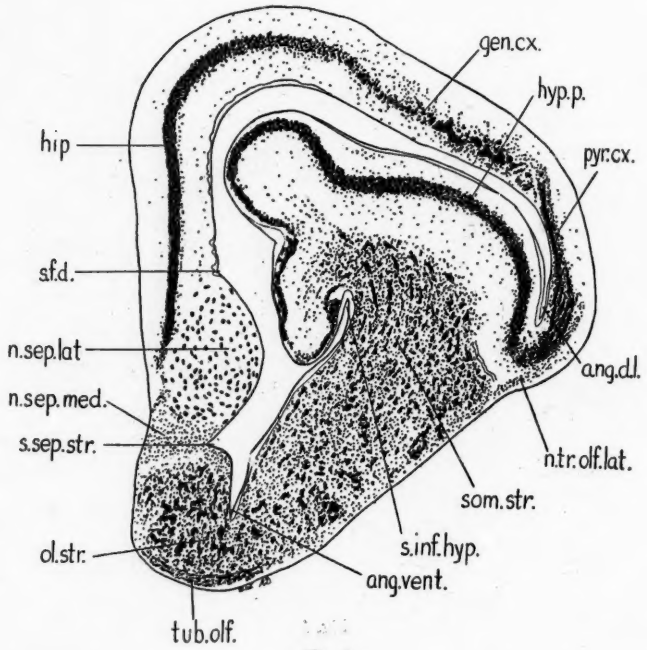
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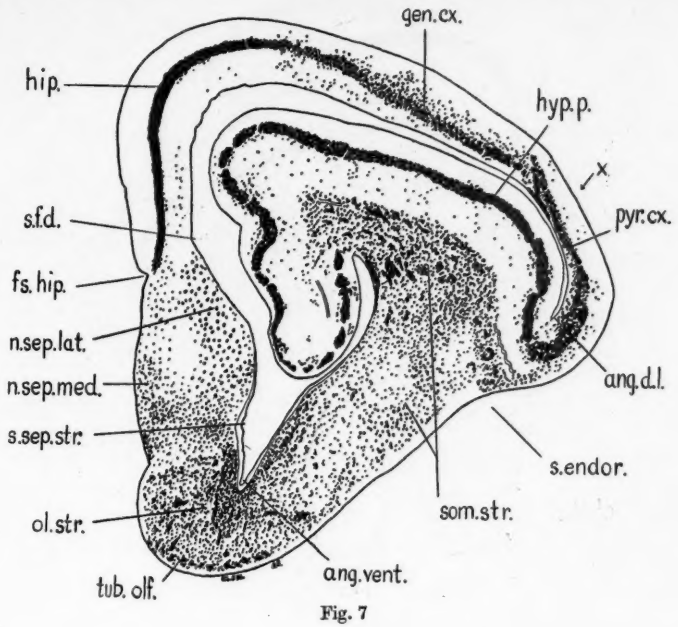
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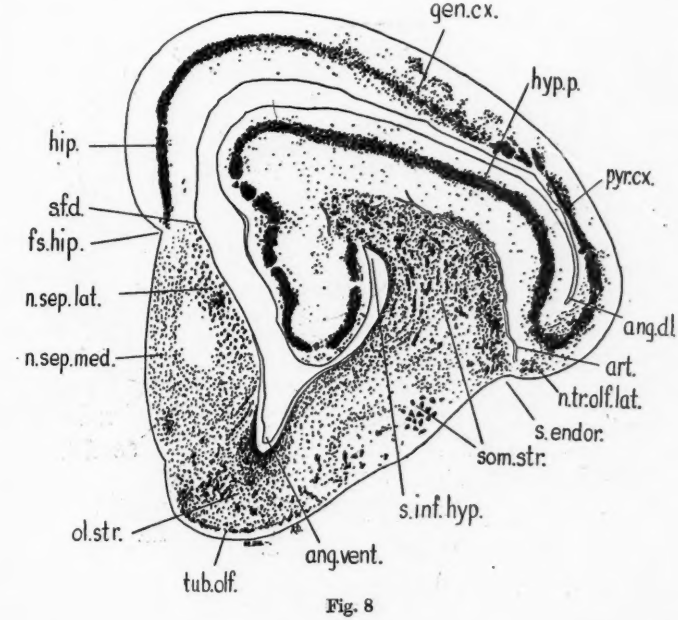
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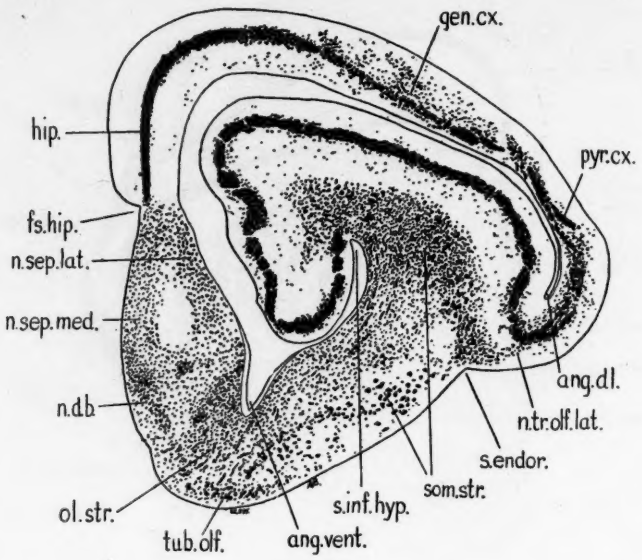
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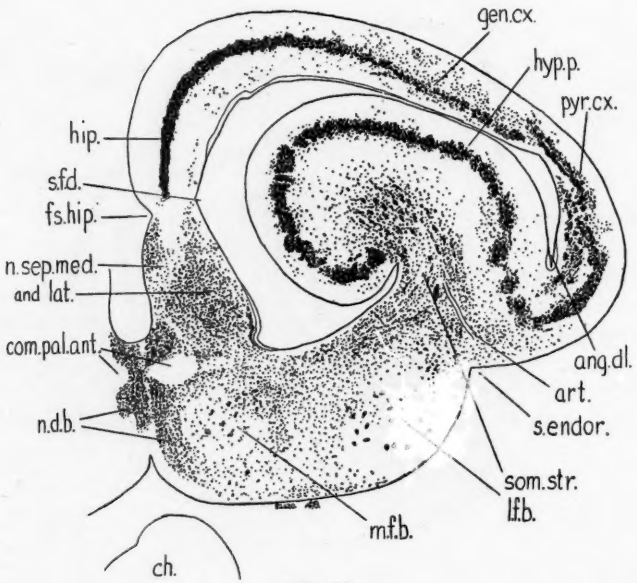
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Fig. 10

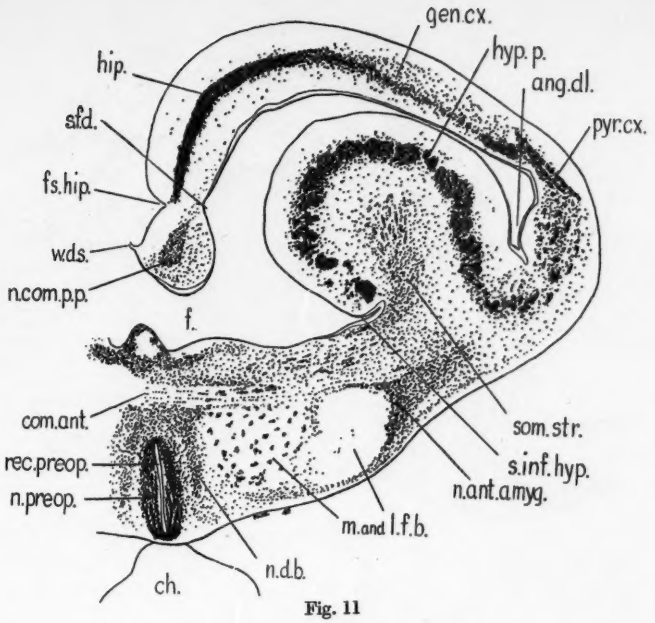
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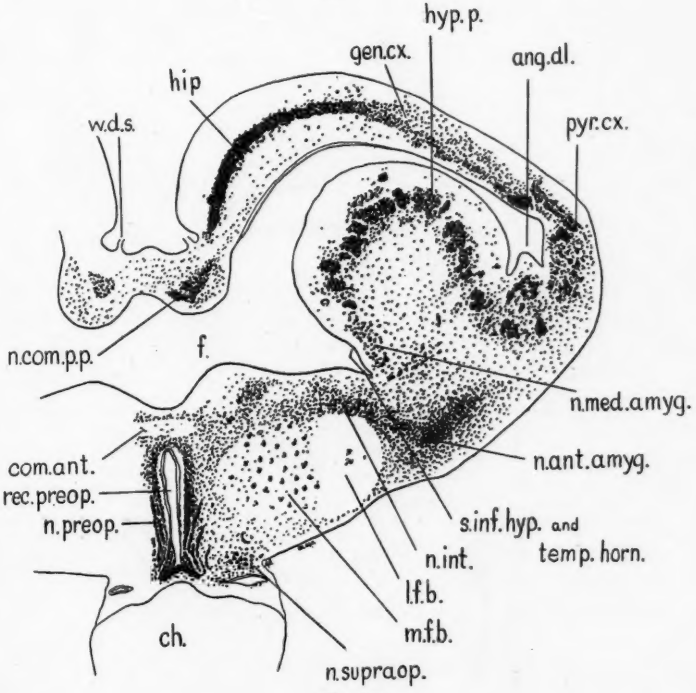
Fig. 11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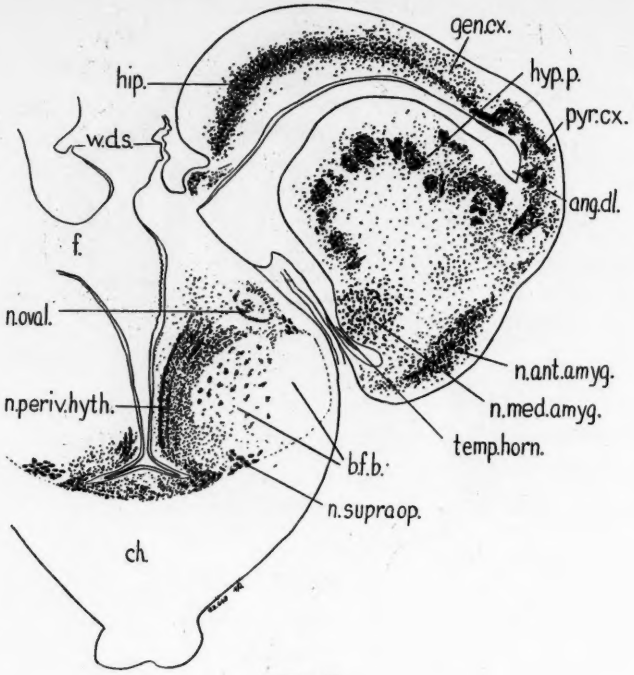
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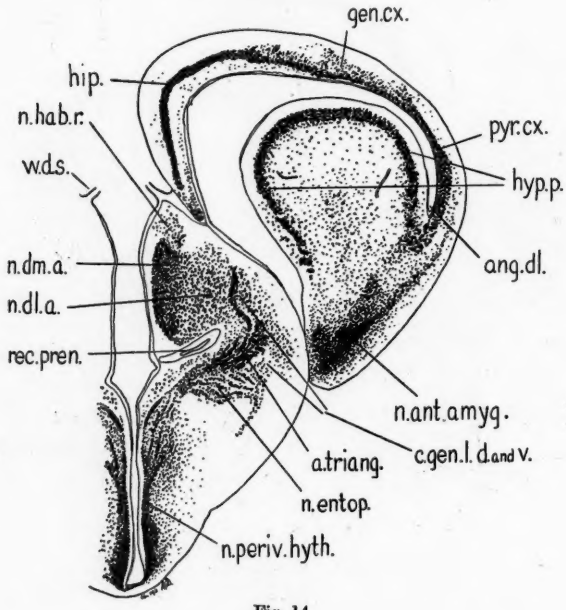
Fig. 13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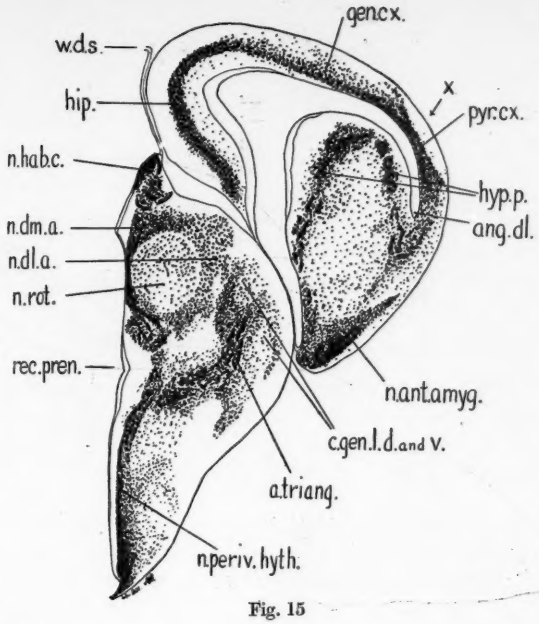

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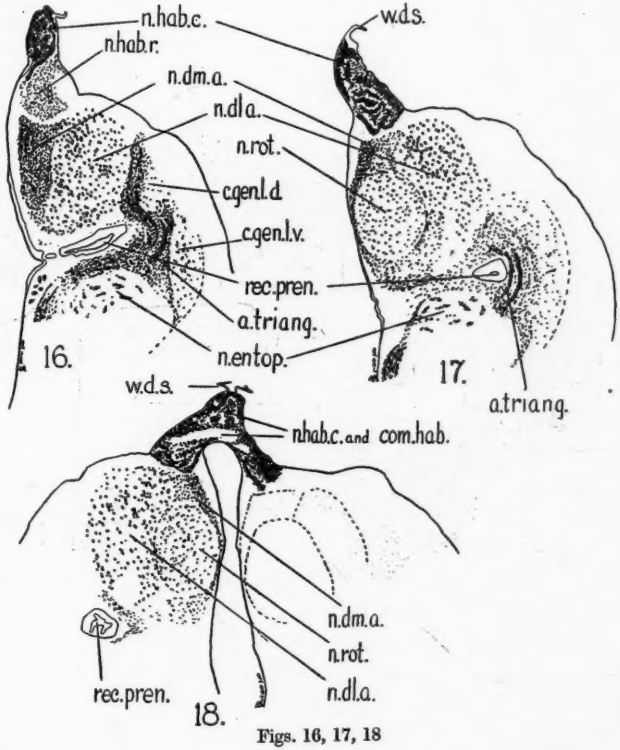
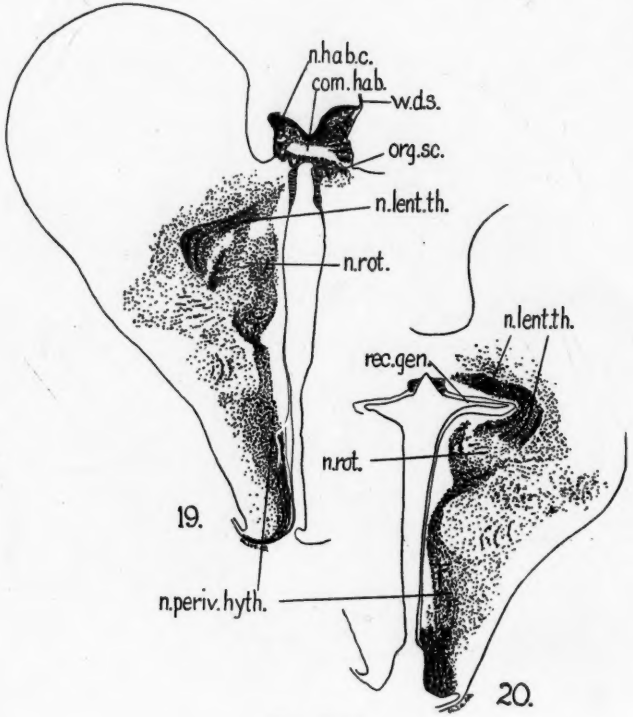
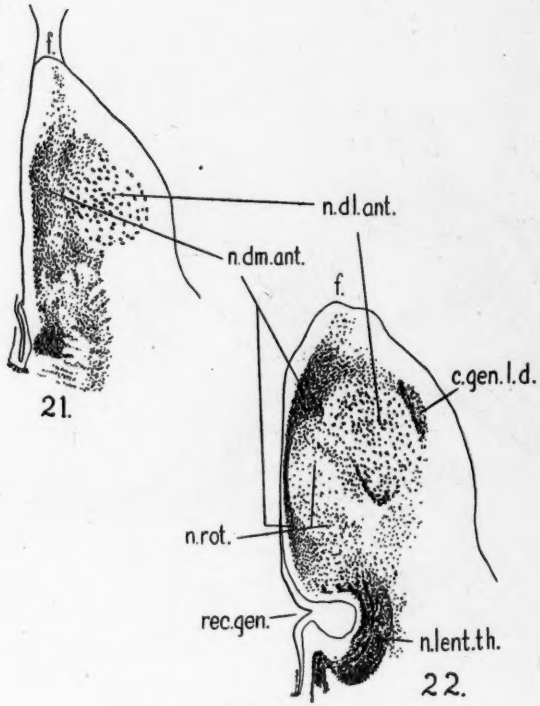


Figs. 16, 17, 18



Figs. 19, 20



Figs. 21, 22

THE ARTERIAL SUPPLY OF THE CEREBRAL CORTEX IN THE CHIMPANZEE (*ANTHROPOPITHECUS TROGLODYTES*)

By JOSEPH L. SHELLSHEAR

Professor of Anatomy, University of Hong Kong

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INTRODUCTION

THE primary function of the arterial system is the carriage of materials to the various organs of the body in accordance with their functional needs. In a series of researches the writer has shown that the arteries, when analysed in terms of their final areas of supply, show a remarkable constancy; and that this constancy of pattern is an important addition to the other methods of determining morphological problems. In the literature dealing with the evolution of the brain, arteries are seldom mentioned; the reason being that arteries are generally regarded as irregular in their distribution, and therefore of little use in the determination of such problems as the evolution of cerebral structures. Elliot Smith (25), however, insisted upon their morphological significance.

The examination of the arteries of the brain of the Chimpanzee, made during the investigation of the middle cerebral artery in Man, revealed so many suggestive features and showed such similarity with the human condition that it seemed desirable to publish an account of them. Hence I submit this preliminary communication on the subject, which is worthy of fuller and more detailed study.

As in the examination of the peripheral nervous system, so also in the examination of the arteries, the origin, the intermediate distribution, and the final supply must each in turn be critically examined. In this paper emphasis is laid on the final supply of the cortical arteries. It is in their intermediate distribution that arteries show a degree of explainable variation; and it is this variation which has detracted from their use in the study of general morphological problems. Modern text-books deal in the main with the larger branches of the arteries. The size of the arteries has been used as the index of their importance; and so the fundamental characteristic of arterial distribution has been overlooked. This characteristic is that arteries are variable in their intermediate distribution but remarkably constant in their final areas of supply. These facts have been hinted at by Evans in his introduction to the development of the vascular system in Keibel and Mall's *Text Book of Embryology* (17) when he says:

"The cause of the early appearance of vessels in a multiple capillary form is consequently to be found in the view that this represents the fundamental method of vascular growth, and that larger vessels only come into existence secondarily when the number of capillaries induces an increased supply of blood. Such an event leads to the enlargement of certain fortuitously situated capillaries into arteries and veins. The larger vessels are to be considered in the light of servants of the capillaries, for which they are but the delivering and draining pipes."

John Hilton (15) first suggested that the distribution of the arteries showed a precision and purpose which seemed to be related with the function of the

part supplied. Charcot (6), with his intimate knowledge of the researches which were being carried out by Duret (9), and in spite of the rudimentary knowledge of his time on the differentiated areas of the cerebral cortex, foresaw the value of a detailed knowledge of the cortical arterial supply. His writings give the impression that he viewed the vascular system from much the same view-point as did Hilton. He advanced the view that the relative autonomy of the vascular areas was a point of capital importance in the study of cerebral localisation:

"This autonomy does not belong exclusively to the large areas; it is found also in the secondary departments into which the former are divided and which correspond to the arterial ramifications of the second and third order. Between these secondary regions, as in the case of the large areas, communications may be possible, but are frequently very difficult....This is a point of capital importance in the study of cerebral localisation."

It is strange that, with this conception, no effort seems to have been made by either Charcot or Duret to analyse and name these arterial ramifications of the second and third order; for the importance of the matter seemed to be obvious to them from the following passage:

"Consequently, we must have a thorough knowledge of each of the principal arteries emanating from the Sylvian, and examine more closely their mode of distribution in the primary convolutions of the region. The Sylvian artery divides into four principal branches, or at least gives origin to four principal branches."

These two observers undoubtedly viewed the distribution of the arteries from the clinical standpoint and so were more particularly concerned with those vessels which were to be regarded as *principal* from this point of view. This one-sided view-point caused the fact to be overlooked, and it still is so, that insignificant branches may be of profound morphological significance. In support of this let us examine the arterial supply of the area orbitalis of Elliot Smith. Its boundaries can be plotted out from the line of demarcation between the anterior and middle cerebral arteries, ascertained from the works of Duret and Beevor, and from the examination of its arterial supply shown in fig. 686 in Gray's *Anatomy* (13) and in fig. 739 in Cunningham's *Anatomy* (8). Again in a paper on the arteries of the brain of the Echidna, at present in process of publication, I have described the posterior pyriform branch of the middle cerebral artery as being limited to the posterior pyriform area in its supply. In Plate II, fig. 7 of this paper the corresponding artery is seen in the Chimpanzee lying internal to the posterior rhinal fissure. From a morphological point of view these insignificant looking vessels are of moment. The aim of the anatomist is to acquire such morphological knowledge, leaving to the clinician to decide on its clinical importance. It is only natural, however, that the clinical view-point should have been emphasised in the past, for it is to the clinicians that we owe practically the whole of our knowledge of cerebral

vascularisation; and so it is from Charcot that the relative value of the branches of the middle cerebral artery is expressed above in the word *principal*. It must be clear, however, that the Sylvian artery has maintained its identity and played its part during the whole drama of the evolution of the cerebral cortex. The cortical branches, which may appear at first sight to be the more important, were relatively late in coming on the stage and may be quite subordinate in importance from the morphological point of view.

MATERIAL AND METHODS

The brain of one Chimpanzee, injected with carmine gelatine, forms the basis of this investigation. Comparison has been made with a large series of Macaque, Gibbon, Orang, and human brains. These were not injected. This is a distinct disadvantage in the case of all except the human brains; and the amount of information obtained was to some extent limited, although of great value when used in comparison with the brain of the Chimpanzee.

The choice of method to be used in the examination of the cortical arteries is an important matter. In many cases one must use the material available and from the nature of the fixation injection is often impossible. In the human brain the non-injected arteries frequently give a clearer picture than the injected, and, although the examination is slower and more tedious, I prefer it. Our object in the examination is the identification of arteries of supply as distinct from arteries of distribution; and it is here desirable to explain by means of a diagram how this separation is attempted and made use of as a method in investigation.

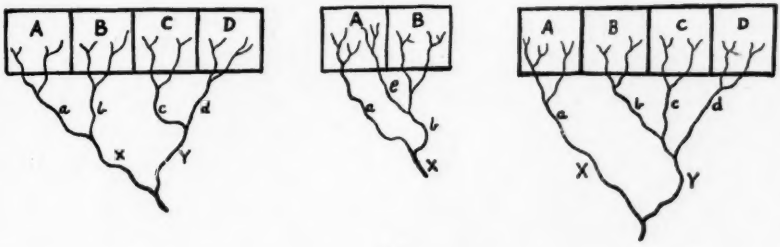
Arteries of supply contrasted with arteries of distribution

Let the areas *A*, *B*, *C*, and *D* in diagram 1 represent defined areas of cerebral cortex supplied by the arteries *a*, *b*, *c*, and *d*. If the area *A* is also supplied by artery *e* in one specimen (diagram 1 A), then it follows that, either the arterial supply to area *A* is variable, or that area *A* is composed of two autonomous vascular areas; in which case the branch *e* to the secondary area A 2 becomes a morphological unit.

If areas *A*, *B*, *C*, and *D* are invariably supplied by the arteries *a*, *b*, *c*, and *d* the supply can be regarded as constant. This is true regardless of the way in which these arteries arrive at their destination. In diagram 1A the areas *A* and *B* derive their blood from the trunk *X*, areas *C* and *D* from the trunk *Y*. In diagram 1C area *A* derives its blood from the trunk *X*, areas *B*, *C*, and *D* from the trunk *Y*. Here *X* and *Y* are examples of variation in distribution, but the areas are supplied by the same arteries.

In this work it is the arteries of the order *a*, *b*, *c*, and *d* which have been used for the purpose of analysis. These have been named and described in terms of their final areas of supply. It is clear that the choice of the supplying

artery must be somewhat arbitrary and that a great deal of observation is necessary to establish the hypothesis that the arteries of supply to the cerebral cortex show a constancy of pattern. In other parts of the brain the existence of arteries limited to areas of definite function has been established. Examples of such autonomous vascular areas are seen in the arterial supply of the anterior nucleus of the thalamus (Beevor(3)), the nucleus of the hypoglossal nerve, the posterior columns of the cord, the vagus nucleus (Stopford(26)), and various structures concerned in the evolution of the forebrain, including numerous circumscribed areas of the cerebral cortex (Shellshear(20, 21, 22)). The analysis of the cortical arteries in the Chimpanzee shows a symmetry on the two sides and a close agreement in the extent of the cortical areas supplied by the corresponding arteries (text-figs. 2, 4).



A B C

Diagram 1. To explain how constancy in supply may occur with variability in distribution.

The charts showing the areas of supply have all been reconstructed from photographs. This method necessitates more figures than Brodmann used, but this has its compensation in their greater value for comparison with pictures of sulci and other structural features. The inaccuracy of the drawing of many charts, and the attempt to put too much on one picture, detracts from their value when used as a basis for comparison.

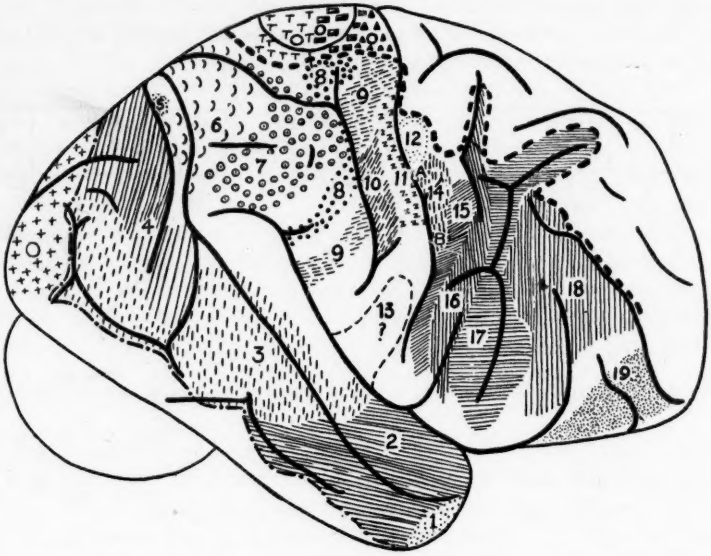
The use of photographs, however, tends to give a false impression of the extent of the areas supplied, since only the surface areas can be depicted, and large hidden areas exist in the submerged walls of the sulci. This is of considerable moment; for the extent of the buried surfaces will vary from brain to brain as do the sulci.

GENERAL DESCRIPTION

The middle cerebral artery

In this section the branches of the middle cerebral artery are described from the points at which they emerge from the fissure of Sylvius to their final destination. The mode of branching of the vessels in relation to the island of Reil will be discussed later.

In text-figs. 2 and 4 the general distribution of the middle cerebral artery is shown on the right and left sides respectively. The line of demarcation between the three major arteries is seen to be in general agreement with the findings of Duret and Beevor. A glance at these figures shows the general symmetry on the two sides. Many of the areas exactly correspond, but it is necessary to appreciate at the outset that the derivations of the arteries supplying them do not of necessity correspond; for example, areas 6 and 7 on the left side are supplied by the common artery which emerges from the

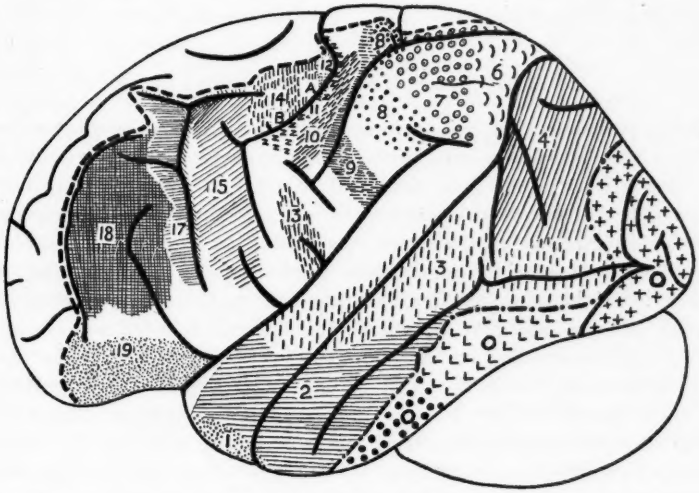


Text-fig. 2. The autonomous vascular areas on the lateral surface of the right hemisphere of the brain of the Chimpanzee.

posterior end of the fissure of Sylvius (Plate I, fig. 3); whereas on the right side the artery, occupying this same position (Plate I, fig. 1), only supplies area 7, area 6 here being supplied in common with area 5. Area 18 is an example of exact correspondence. Its artery of supply emerges from the sulcus fronto-orbitalis and forms anteriorly the line of demarcation between the anterior and middle cerebral arteries along a line which corresponds with the position of the sulcus rectus. This artery allows the sulcus rectus to be identified in the higher anthropoid apes and frequently in Man. This question of making use of the arterial supply as a means of determining sulcal homologies will be discussed later.

The branches of the middle cerebral artery

The posterior pyriform branch (Area 21). In a study of the arteries of the brain of the Echidna the analysis of the branches of the middle cerebral artery shows the pyriform area to be supplied by three arteries, which I named the anterior, middle, and posterior pyriform arteries. The posterior pyriform artery supplies the pyriform area bordering the posterior rhinal fissure and is definitely limited by that fissure laterally. In the Chimpanzee (Plate II, fig. 7, and text-fig. 8) the first cortical branch of the middle cerebral artery corresponds in every way with this artery in the Echidna. On the right side it arises from



Text-fig. 4. The autonomous vascular areas on the lateral surface of the left hemisphere of the brain of the Chimpanzee.

the stem of the middle cerebral artery, and on the left side from the point of junction between the internal carotid and middle cerebral arteries. It takes a somewhat tortuous course on the limen insulae and then proceeds backwards to supply a small area of cortex lying medial to the posterior rhinal fissure. The posterior limit of its supply forms the boundary between the middle and posterior cerebral arteries in this region.

The temporo-polar branch (Area 1). This small branch, like the preceding branch, has an independent origin from the middle cerebral artery. It arises proximal to the point at which the lateral striate arteries arise. The temporo-polar branch has been previously described by me in the Orang-utan (1927 *a*) and in Man (1927 *b*). In text-fig. 16, showing the arteries of the base of the brain in the Common Macaque, this branch is also shown. Its relations and area of supply in the brain of the Chimpanzee agree in every way with the condition

in the Macaque, Orang and Man. On reflecting the temporal pole, it is seen lying on the dorsal surface of the temporal pole whence it turns on to the lateral surface and supplies the anterior end of the temporal gyri. The area of the vascular supply is numbered 1 (text-figs. 2 and 4). This area coincides very closely with the area temporo-polaris of Elliot Smith, the area 38 of Brodmann and the area 39 of Mauss. Since this area enters into the formation of the line of demarcation between the middle and posterior cerebral arteries, its presence as an autonomous vascular area finds, in part, confirmation from the writings of Duret and Beevor. These authors both agree in finding that the anterior end of the temporal lobe is supplied by the middle cerebral artery. The constancy of this supply would seem to indicate that there is in this region little anastomosis between the different arteries.

The temporal branches (Areas 2 and 3)

A comparison of the specimen under consideration with a number of human brains shows that the temporal branches can be divided into an anterior and a posterior series. On the right side (Plate I, fig. 1) the anterior and posterior temporal branches emerge separately from the fissure of Sylvius; whereas on the left side (Plate I, fig. 3) the posterior part of the anterior temporal branch arises from the posterior temporal branch at the point of emergence. Area 2 then on the right side (text-fig. 2) is supplied by the anterior artery which at once divides into two branches. On the left side the same extent of cortical area is supplied by an independent anterior artery and the branch above-mentioned. The difference in the method of origin and distribution does not affect the extent of the area of supply. The area of supply of the anterior temporal branch (area 2) is bounded anteriorly by the posterior limit of the area temporo-polaris; inferiorly it forms the line of demarcation between the middle and posterior cerebral systems along a line which forms the upper limit of supply of the anterior temporal branch of the posterior cerebral artery. This line passes along the inferior temporal gyrus. Posteriorly the limit of area 2 runs obliquely backwards to a point close to the posterior end of the middle temporal sulcus. The inferior boundary of the area coincides with the line separating areas 20 and 21 of Brodmann; otherwise the area does not appear to correspond with any distinctive area, sharing with the posterior temporal branch the supply of areas 21 and 22 of Brodmann.

In Plate I, fig. 3 there is seen to be a considerable anastomosis between the anterior temporal branches of the middle and posterior cerebral arteries on the surface of the inferior temporal convolution. Similar anastomotic vessels are found in the human brain in this situation; and this may account for the amount of variation which Beevor here found in the distribution as indicated by the colour of the injection. Unfortunately he did not say that the line of colour demarcation agreed with the line of vascular demarcation, determined by observation of the vessels themselves.

The posterior temporal branch (Area 3). Emerging from the fissure of Sylvius on a level with the lower end of the sulcus centralis, this vessel crosses the superior temporal convolution obliquely and enters the parallel sulcus. It courses in the depth of this sulcus for some distance and, lying in it, gives rise to two branches. The anterior of these crosses the middle temporal convolution and ends within a pocket formed by the posterior end of the middle temporal sulcus and the anterior end of the inferior occipital sulcus. It here anastomoses freely with the posterior temporal branches of the posterior cerebral artery. The posterior branch of the main vessel crosses the angular-shaped gyrus which is wedged between the parallel sulcus and the downwardly directed arm which springs from it; the branch then curves under the outer extremity of the sulcus lunatus and follows the sulcus occipitalis inferior for some distance. Compare its course and relations with the left side of the human brain shown in Plate IV, fig. 12 and observe that the downwardly directed limb of the parallel sulcus in the Chimpanzee is homologous with the inferior element of the anterior occipital sulcus in the human brain. The arteries thus furnish confirmatory evidence of the reality of the homologies determined by other morphological methods ((23), 1927 *c*). The area supplied by this branch of the posterior temporal branch is shown in text-figs. 2 and 4 as the posterior region of area 3. The form and relations of this area are the same on the two sides; it includes the posterior part of the middle temporal convolution and extends backwards into the inferior occipital region. It also supplies the superior temporal convolution immediately bordering on the parallel sulcus, but does not include that region of the superior temporal convolution which borders on the posterior part of the fissure of Sylvius. This area is shown in the figures as a crescentic-shaped area corresponding in form and position with the area circumambiens of Elliot Smith (fig. 562, Cunningham's *Anatomy*, 1922). This area is supplied by branches from the vessel which is seen crossing the posterior end of the superior temporal convolution in Plate I, fig. 1. I have confirmed this method of supply of the auditory area in many human brains and have never found it to be supplied by the posterior temporal branch. On account of the uncertainty of being able to determine a particular branch to this area it is left blank in the charts; but by process of exclusion one is justified in regarding it as an autonomous vascular area, although its separate involvement in a vascular lesion would appear to be unlikely. These anatomical features receive full confirmation from the clinical observations of Adolf Meyer(18). The reader is here referred to the figures of his paper, and in particular to his figs. 2, 5, 7 and 12. His fig. 12 shows area 3 demarcated by a vascular lesion.

The problem of discriminating between arteries of distribution and arteries of supply now presents itself; for on the left side of the brain of the Chimpanzee the posterior temporal branch is entirely confined in its supply to area 3 (text-fig. 4), whereas on the right side area 4 is supplied by a branch of the posterior temporal branch of the middle cerebral artery. On this side, after giving off the posterior branch above described to supply the posterior region

of area 3, the artery continues along the parallel sulcus and then, turning downward in the downwardly directed limb of that sulcus for a short distance, crosses to the lower end of the sulcus lunatus and supplies area 4 (text-fig. 2). On the left side the corresponding area 4 is supplied by a branch of the middle cerebral artery, which is seen crossing the posterior end of the superior temporal convolution in Plate I, fig. 3. Does the variation in distribution discountenance the hypothesis of constancy in supply? It seems to the writer that the variation permits of the determination of the separate autonomous area 4, for the form of this area is the same on the two sides and a reference to Plate III, fig. 9, shows that the relations of the terminal branches in this area to the superior occipital sulcus are in every respect similar. The type of variation in distribution is in every way parallel with the type of variation found in the distribution of such an artery as the posterior inferior cerebellar artery. It was this latter type of variation which suggested the use of the diagram for explanatory purposes in the introduction to this paper.

The parietal branches

The encroachment on the parietal area by the shelf-like lunate operculum made the examination of these branches very tedious; nevertheless each branch could be traced to its termination. It was not possible however to give adequate expression of the extent of their supply by means of charts. For this reason, and also as this paper is intended as a preliminary communication to the description of the cortical arteries in Man, the distribution in the human brain is shown in Plates III and IV, figs. 11 and 12. These figures accurately portray what might be termed the average condition in the human brain, and so this specimen is here used for comparative purposes. Before, however, entering into the discussion of the parietal branches in the Chimpanzee, it is here desirable to give a brief account of the arrangement of the sulci of the parietal and occipital lobes in this specimen.

A mere glance at Plate I, figs. 1 and 3, by anyone acquainted with the form of the occipital lobe in the higher apes will show that we are here dealing with an unusual specimen. On the left side the forward position of the lunate operculum so as to cover over the ascending part of the parallel sulcus is a condition which I have not hitherto seen described. The occipital operculum illustrates an extreme circopithecoid condition. It extends forward as a thinned shelf completely hiding from view on the left side the whole of the upper end of the parallel sulcus, and on the right side this sulcus is only a few millimetres in front of it. The parallel sulcus has the same form on both sides. It extends directly upwards into the angle formed by the intraparietal and lunate sulci in typical circopithecoid fashion. On both sides the parallel sulcus gives off posteriorly the downwardly directed arm, already spoken of, which is the homologue of the lower part of the anterior occipital sulcus. This sulcus is well shown on both sides of the human brain in Plates III and IV, figs. 11 and 12. In the supramarginal gyrus, immediately above the posterior end of the fissure

of Sylvius, there is a sulcus lying at right angles to the ascending part of the parallel sulcus. This might give the impression of joining the parallel sulcus and of similating the form of parallel sulcus seen in the Gorilla; such is not the case, however, for it is merely a shallow depression. Medially the occipital operculum covers over the parieto-occipital sulcus on both sides.

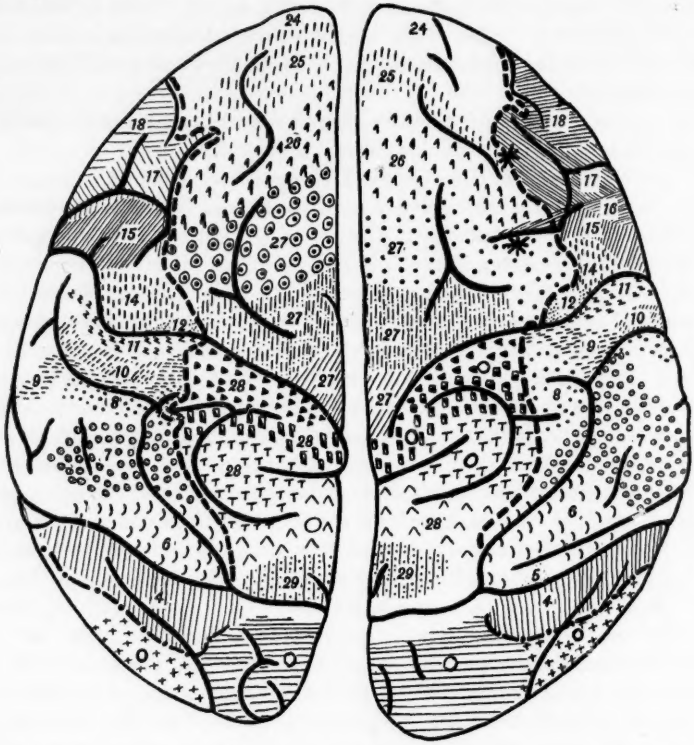
The superior occipital sulcus is long and passes well forward on the surface of the operculum. On the left side its posterior extremity is bifurcated, on the right side it is a simple straight sulcus (Plate III, fig. 9). It is to be noted that the vascular relations to this sulcus are the same on both sides and also that the anterior end of the sulcus lies within the middle cerebral area. This will be discussed later.

For the purpose of description the parietal branches are named tentatively the anterior, middle, and posterior parietal branches.

The posterior parietal branch (Area 5). The area supplied by this artery lies posterior to the parallel sulcus and so no part of it can be shown in text-fig. 4 and only a small part in text-fig. 2. The area, lying posterior to the upper end of the parallel sulcus, extends upwards under cover of the occipital operculum to include the region of the transverse occipital sulcus. Its extent in the Chimpanzee would appear to correspond with the region of the gyrus postparietalis of human anatomy. The artery supplying this area arises differently on the two sides. In Plate I, figs. 1 and 3, a large artery is seen crossing the posterior region of the superior temporal convolution obliquely; it lies a short distance anterior to the posterior end of the fissure of Sylvius. This artery is of what we may call stem value; for the arteries of supply arising from it are different on the two sides. On the left side it divides into two branches; the posterior of these corresponds in every way with the continuation of the posterior temporal branch which supplies area 4; the anterior branch is the posterior parietal branch and supplies area 5. Thus on the left side it divides to supply areas 4 and 5. On the right side the artery crosses the superior temporal convolution in the same way and then enters the parallel sulcus. It also divides into two branches but in this case it is the posterior branch which supplies area 5; the anterior branch supplies area 6 and constitutes the middle parietal branch. This analysis is confirmed in the examination of the human brain, in which one of the most constant landmarks is the presence of an artery emerging from the inferior element of the bifid posterior extremity of the fissure of Sylvius. This vessel crosses the superior temporal convolution and in practically every case leaves a well-marked indentation on the gyrus. It is seen in both Plates III and IV, figs. 11 and 12.

The middle parietal artery (Area 6). The difference in origin of this artery on the two sides can be readily understood by examining Plate I, figs. 1 and 3. In fig. 1 of the right side an artery emerges from the posterior end of the fissure of Sylvius, and passes directly upwards to the sulcus intraparietalis; whereas on the left side (fig. 3) the artery emerging from approximately the same position curves backwards to the parallel sulcus. Here it gives off a

large branch which passes into the parallel sulcus. The continuation of the main stem corresponds with the artery on the opposite side. The branch which passes into the parallel sulcus is the middle parietal branch. It supplies both walls of the ascending portion of this sulcus and the cortex surrounding its upper extremity (Plate II, fig. 5 and text-fig. 6). Area 6, then, supplied by the middle parietal artery, is closely related with the gyrus angularis of human anatomy.



Text-fig. 6. Chart of the autonomous vascular areas on the dorsal surface of the brain of the Chimpanzee.

The anterior parietal artery (Area 7). This artery emerges from the posterior end of the fissure of Sylvius and passes upwards to the sulcus intraparietalis. It supplies both walls of this sulcus as far forward as the junction of the intraparietal sulcus with the inferior postcentral sulcus. Its area of supply is numbered 7 in the figures, and it will be noted that this area extends above the limit of the intraparietal sulcus into the superior parietal lobule, through which therefore the line of demarcation between the middle and anterior cerebral arteries runs. The area of supply is thus somewhat more extensive

than the gyrus supramarginalis of human anatomy. The presence of anastomotic connections at the periphery of the parietal areas of supply could not be determined in the brain of the Chimpanzee; in the human brain shown in Plates III and IV, figs. 11 and 12, however, there were large anastomotic channels between the anterior and middle cerebral areas. The sites of these anastomoses are shown by asterisks in the figures.

The postcentral branches

These branches are tentatively named the anterior, middle, and posterior postcentral branches. They emerge in series from the posterior third of the fissure of Sylvius and proceed to the sulcus postcentralis inferior.

The posterior postcentral branch (Area 8). The relations and extent of supply of this vessel correspond on the two sides. It emerges from the anterior terminal limb of the fissure of Sylvius and passes forwards to enter the sulcus postcentralis inferior (Plate I, fig. 1). It supplies area 8. This area includes a narrow strip of cortex lying posterior to the sulcus postcentralis inferior, the posterior wall of this sulcus in its upper two-thirds, and the area of cortex immediately surrounding its upper extremity. The extent of cortex supplied is larger than the figures indicate, for the sulcus is relatively deep. The relations of the upper end of the sulcus postcentralis are well shown in text-fig. 6. It is joined to the sulcus intraparietalis on both sides, whereas the sulcus postcentralis superior is independent. This figure shows a sulcus forming three parts of a circle in the superior parietal lobule. In the concavity of this sulcus lies the posterior end of the sulcus cinguli. On both sides there is given off from the curved sulcus a branch which comes into relation with the upper end of the sulcus postcentralis inferior; this branch is the lower end of the sulcus postcentralis superior. The form of the sulci shown in this specimen is quite characteristic and is closely similated by specimens in the collection of the Museum of the Royal College of Surgeons. The significance of these sulci will be more fully appreciated after the branches of the anterior cerebral artery are described. On the right side the inferior end of the sulcus postcentralis superior lies behind the upper end of the sulcus postcentralis inferior and is entirely separated from it by a narrow gyrus. On the left side the two sulci are in line with one another, and a forking of the upper end of the sulcus postcentralis inferior is thereby produced. The two sulci are here also separated from one another by a narrow gyrus; but in this case the narrow gyrus is submerged to some extent. This narrow gyrus, on both sides, forms the upper limit of the supply of the posterior postcentral branch, and the line of demarcation in this region between the anterior and middle cerebral systems. It was not possible to determine the extent of the anastomosis between the two systems at this point in the Chimpanzee. In the human brain, however, there are well-marked inosculating channels across the line of demarcation.

The middle postcentral branch (Area 9). This branch emerges from the fissure of Sylvius a short distance anterior to the posterior branch. It crosses

the lower end of the gyrus between the Sylvian and inferior postcentral sulci and enters the latter sulcus from the posterior aspect. Its area of supply is identical on both sides. It crosses the bottom of the sulcus and passes up its anterior wall. The terminal branches may be seen emerging from the anterior wall in Plate I, figs. 1 and 3, close to the point at which the sulcus is joined to the sulcus intraparietalis. Its area of supply includes practically the whole extent of the anterior wall of the sulcus postcentralis inferior and the area of cortex on the surface which is numbered 9 (text-figs. 2, 4 and 6).

The anterior postcentral branch (Areas 10 and 11). This branch is a very interesting one, on account of the variations which it shows. The type of variation is the same in the brain of the Chimpanzee as it is in the human brain. If one compares Plate I, figs. 1, 3, and Plate IV, fig. 12, an artery—the middle central branch—is seen to enter the lower end of the sulcus centralis. This branch is a very constant one in the brain of the anthropoids and acts as a very important landmark. In Plate I, fig. 1, an artery is seen to enter the sulcus centralis from the posterior aspect immediately above the middle central branch. This artery emerges from the fissure of Sylvius through the sulcus subcentralis posterior. It is the posterior central branch. In many brains it appears to be absent; thus in Plate I, fig. 3, it seems to be represented by an insignificant twig supplying the lower end of the postcentral gyrus. Immediately posterior to it an artery crosses the lower bifurcated extremity of the sulcus postcentralis inferior and proceeds to the posterior aspect of the sulcus centralis. In the specimens this artery sends a twig up the centre of the gyrus postcentralis (area 10 in the figures), and at the sulcus centralis sends a large branch along the anterior border of the gyrus postcentralis close to the sulcus centralis; finally in Plate I, fig. 3 and Plate IV, fig. 12 a large branch is given to the sulcus centralis at the point at which the branch to the anterior region of the gyrus postcentralis arises. The area supplied by this branch which enters the sulcus centralis agrees in every way with the area supplied by the independent posterior central branch in Plate I, fig. 1. The branch which is named the anterior postcentral branch then excludes this branch which enters the sulcus centralis. The arrangement of these arteries gives expression to the difficulties involved in the analysis of the arteries; and yet at the same time, provided that the classifications here made in the beginnings of the investigations are not taken too rigidly, it everywhere points to the general principles underlying vascular distribution.

Thus, while my observations on the human brain are not yet sufficient to warrant a final opinion as to the analysis of these arteries, they have progressed sufficiently far to warrant the tentative classification put forward. The close parallel between the arterial supply of the visual area and its histological boundaries leads to the comparison of the blood supply of the gyrus postcentralis with its structural boundaries. A reference to the figures of Brodmann and Elliot Smith suggests a similar close relationship between the arteries and the structures supplied. For this reason the artery which passes

up the anterior edge of the gyrus postcentralis is named the anterior postcentral branch. It is closely related to area 3 of Brodmann. In the human brain (Plate IV, fig. 12) this artery follows the anterior edge of the gyrus postcentralis as far as the anterior cerebral area, where it enters into direct inosculation with a branch of the anterior cerebral artery. Unfortunately the brittleness of the arteries in the brain of the Chimpanzee, after injection with carmine gelatine, prevented my obtaining certain evidence of the sites of inosculation except in a few instances. The anterior postcentral branch, in passing up the anterior edge of the gyrus postcentralis, sends branches to supply the whole of the posterior wall of the sulcus centralis and in both the brain of the Chimpanzee and Man branches could also be traced to the anterior wall of this sulcus; so that this artery takes a share in the supply of the motor cortex.

The middle cerebral supply of the Rolandic area

The supply of the gyrus praecentralis is very complex; and yet the examination of this brain, with the large series which I have had at my disposal for comparison, shows a considerable degree of uniformity. Nevertheless, on account of the complexity, the description here given can only be regarded as tentative to act as a foundation for the more extended researches which are being taken in hand.

The arteries are named the anterior, middle, and posterior central branches of the middle cerebral artery. Their method of entering the sulcus centralis in Man and the Chimpanzee, as well as their final areas of supply, shows a considerable degree of constancy. Such differences as exist, tend rather to accentuate their constancy than otherwise. The middle central branch we have seen entering the lower end of the central sulcus; the posterior central branch entering the same sulcus somewhat posteriorly, either as an independent artery or as a branch of the anterior postcentral branch. The anterior central branch is a small one which supplies the lower third of the gyrus praecentralis. This vessel may arise from the posterior inferior frontal branch of the middle cerebral artery or from the middle central branch.

The posterior central branch (Area 12). This artery arises in the manner described above. It enters the sulcus centralis from the posterior aspect and then passes to the anterior wall of this sulcus. It supplies the anterior wall over an area indicated by the letters *A* and *B* in text-figs. 2 and 4, and then emerges to supply the area of precentral cortex numbered 12. It forms the line of demarcation between the anterior and middle cerebral arteries in this region. It was not possible to determine whether anastomosis occurred across this line of demarcation in the Chimpanzee; in the human brain (Plate IV, fig. 12) there is a well-marked anastomosis between this vessel and a branch of the anterior cerebral which crosses the sulcus praecentralis superior.

In text-fig. 4, the area numbered 13, supplied by an independent branch related to the sulcus subcentralis posterior, is shown. The presence of this independent area on the left side draws attention to a difference in the two

sides of the brain which has frequently been observed by me—a difference which may throw light on the difference in the method of branching on the two sides. The distance between the posterior end of the fissure of Sylvius and the lower end of the sulcus centralis is commonly greater on the right side than it is on the left. There is a resultant bunching up of the sulci on the left side when compared with the right; and a corresponding widening out of the sulci of the inferior frontal gyrus on the same side. Such a bunching of the sulci, with a shortening of the parietal operculum on the left side, tends to cause a grouping together of the arteries within the telescoped sulci subcentralis posterior and postcentralis inferior. It is suggested that this might lead to a difference in the pattern of distribution.

The middle central branch (Area 14). The middle central branch is one of the most constant branches of the middle cerebral artery. It enters the lower end of the sulcus centralis and passing up the sulcus emerges at the upper bend of the inferior genu. It supplies the cortex on the anterior wall of the sulcus below the area supplied by the posterior central branch and the superficial area of cortex numbered 14 in the figures. This area closely corresponds with the area for arm movements figured by Sherrington (24). In the human brain (Plate IV, fig. 12) this artery is seen to pass forwards into the sulcus praecentralis intermedius, whose posterior wall it supplies.

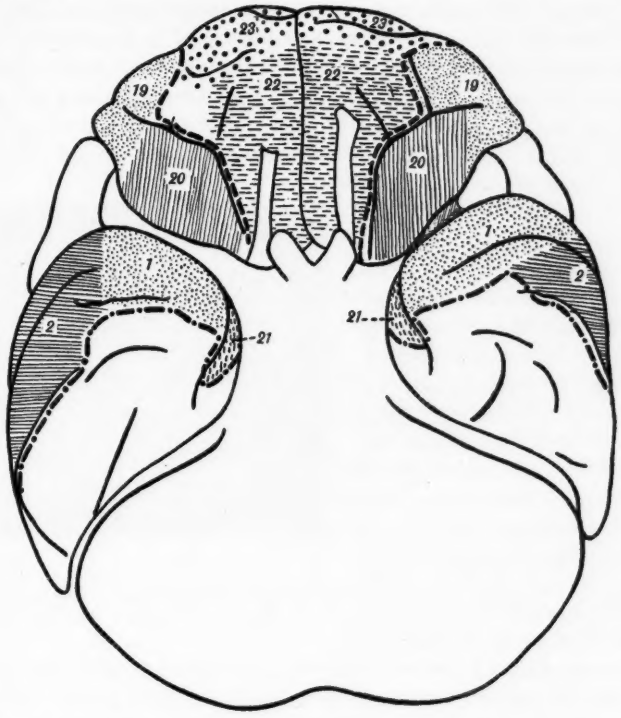
The anterior central branch (Area 15). The arterial supply of the lower third of the gyrus praecentralis seems to be intimately connected with the arterial supply of the posterior part of the inferior frontal gyrus; and it is not always possible to determine the presence of a particular artery to this region. On both sides of the brain of the Chimpanzee and on the right side of the human brain (Plate III, fig. 11) there is a definite artery supplying this area. On the left side of the human brain however the supply is shared by the middle central and posterior inferior frontal arteries. In the Chimpanzee the anterior central branch comes to the surface through the sulcus subcentralis anterior. It supplies the lower third of the gyrus praecentralis as far as the area supplied by the middle central artery. Its area of supply is thus limited to the area for movements of the head and neck.

The frontal branches

This group comprises five arteries, each of which has a clearly defined area of supply in relation to the sulci of the frontal lobe. This relationship is so clear in the majority of cases that indications are given of the changes which have taken place in the evolution of this region and the homologies of the sulci can thereby be suggested. It is convenient to begin the description with the most anterior branch and work backwards.

The orbital branch (Area 20). Since the area of supply of this artery immediately adjoins the anterior cerebral area on the orbital surface of the frontal lobe, its medial limit of supply can be determined from the writings of those who have described the limits of supply of the three major arteries.

In the Chimpanzee the orbital branch arises in common with or in close proximity to the lateral striate group of branches. In Plate II, fig. 7, it is to be seen passing to the curved sulcus orbitalis; and its area of supply is numbered 20 in text-fig. 8. On the left side the artery is an independent branch of the middle cerebral artery; whereas on the right side it arises in common with the next branch to be described—the fronto-marginal branch.



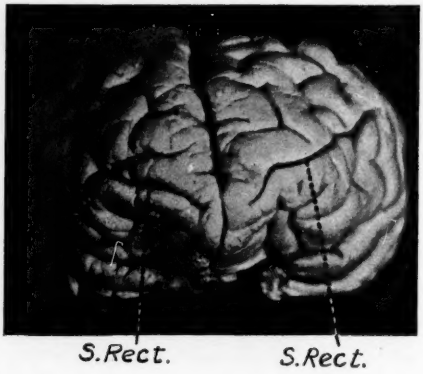
Text-fig. 8. Chart showing autonomous vascular areas on the ventral aspect of the brain of the Chimpanzee.

This area is a very important one on which to concentrate our attention; for it is so clearly an autonomous vascular area in the sense used by Charcot. The vessel itself is depicted in most text-books of anatomy (*vide* Gray, fig. 686 (1926); Cunningham, fig. 739 (1922)). The line of demarcation between the anterior and middle cerebral arteries in this region indicates the inner boundary of the area. This boundary is very constant and is clearly shown in the works of Beevor and Duret (*vide* Beevor, fig. 18 (1909); and Charcot, fig. 7 (1883)). This vascular boundary coincides with the line of demarcation between the areae orbitalis and praefrontalis of Elliot Smith. In the brain of the Chinese,

described by me (1927 *b*), the vascular autonomous area actually took the same form as the area orbitalis depicted by Elliot Smith (Cunningham, fig. 552 (1922)).

The fronto-marginal branch (Area 19). This branch emerges from the fronto-orbital sulcus at the point where this sulcus passes to the lateral surface of the hemisphere. It crosses the lateral end of the sulcus orbitalis and extends as far forward as the anterior end of the sulcus rectus. The area of supply is numbered 19 and closely corresponds with the area fronto-marginalis of Elliot Smith. I have confirmed these observations in a number of human brains.

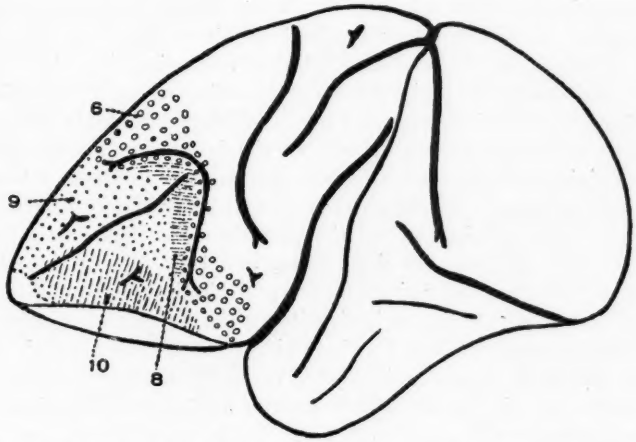
The anterior inferior frontal branch (Area 18). This branch emerges from the outer end of the sulcus fronto-orbitalis. It may emerge in the form of a single artery or as two separate branches (Plate I, figs. 1 and 3). Its area of supply is numbered 18. It will be seen that the general relations and form of this area are the same on the two sides. Particular importance attaches itself to this distribution on account of its easily ascertained correspondence in all the brains which I have examined; furthermore the constancy of its relations to the sulci of the frontal lobe throws light on the changes which have taken place in the evolution of this area. In Plate V, fig. 14, the distribution in the brain of *Cercopithecus mona* is shown. The area of the supply of the anterior inferior frontal branch is limited antero-superiorly by the sulcus rectus. The same relations are found in the Gibbon, Orang and other brains. In the Chimpanzee the antero-superior limit of its distribution is the slightly curved sulcus which extends forwards to the frontal pole. Text-fig. 10 shows the relations of this same sulcus in the Orang taken from the anterior aspect. There can be no doubt that this sulcus is the sulcus rectus; but this question of the institution of homologies will be discussed later (Plate IV, fig. 13).



Text-fig. 10. The sulcus rectus seen from the anterior aspect in the brain of the Orang-utan.

The middle inferior frontal branch (Area 17). In the Gibbon and Macaque this vessel, on coming to the lateral surface, enters the inferior extremity of the sulcus arcuatus. In the Chimpanzee (Plate I, fig. 1) the artery lies immediately anterior to the level of the temporal pole of the hemisphere. It passes over the lower border of the frontal lobe and enters the inferior end of a sulcus which passes obliquely forward and upwards on the surface of the frontal lobe to terminate above the posterior end of the sulcus rectus. Reasons for naming this sulcus the sulcus arcuatus will be given later. Similar relationships are

shown in Plate I, fig. 3. The artery follows the vertical sulcus and is finally distributed to the area surrounding its anteriorly directed upper extremity (area 17). It will thus be seen that the supply of this artery extends to a higher level than that of the anterior inferior frontal artery. This causes the line of demarcation between the anterior and middle cerebral arteries to become irregular at this point. Plate V, fig. 14, of the brain of *Cercopithecus mona*, shows the same irregularity in the line of demarcation; for the area supplied by the middle inferior frontal artery extends upwards in the curve of the arcuate sulcus. Text-fig. 15 is taken from Brodmann's fig. 90(4) to save reference. It shows the histologically defined areas of the cerebral cortex in



Text-fig. 15. This figure is taken from fig. 90 of Brodmann to show the cortical areas related to the arcuate and rectus sulci. Compare with text-figs. 2, 4 and Plate V, fig. 14.

this region; and it is to be noted that his area 8 passes behind the posterior end of the rectus sulcus and extends to the upper end of the arcuate sulcus in exactly the same way as the area of vascular supply does.

In Plate I, fig. 3, a small sulcus is seen arising from the arcuate anteriorly. This sulcus passes forwards and lies under the posterior end of the sulcus rectus. When the condition in the human brain is discussed grounds will be stated for regarding this sulcus as the inferior frontal sulcus of human anatomy. It must here be regarded as a compensatory sulcus, for the vessels (Plate I, fig. 3) are seen to pass right across it to reach their final destinations. By observing the relationships of the arteries to the sulci hints may be obtained as to the identity of the sulci; for example, such arteries as the middle central branch and the middle inferior frontal branch pass into the extremities of sulci; others, such as the posterior temporal and the posterior central branches, enter the sulci from the side and pass into them for some distance: others

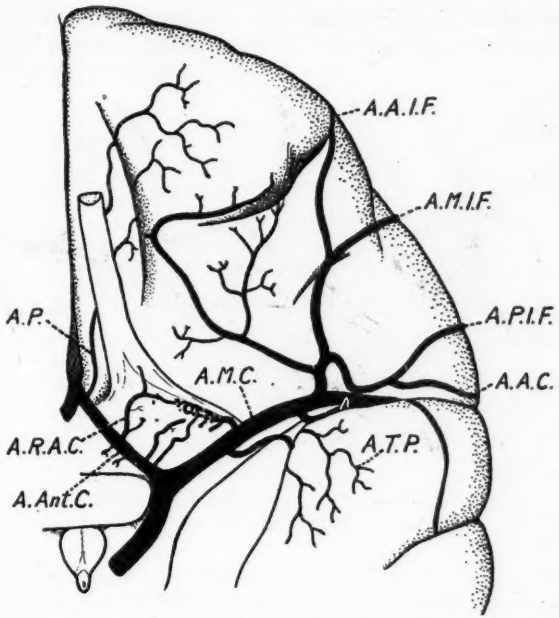
again, such as the anterior postcentral and anterior inferior frontal, pass across the sulci more or less superficially without being buried by them.

On both sides of the brain of the Chimpanzee there are inosculations between the middle inferior frontal branch of the middle cerebral artery and the middle superior frontal branch of the anterior cerebral artery at the line of demarcation between the two major arteries. Free anastomosis similarly takes place between arteries in the corresponding region in the human brain.

The posterior inferior frontal branch (Area 16). On the right side (Plate I, fig. 1) this vessel is seen passing vertically up the frontal lobe between the central and arcuate sulci. In text-fig. 2 its area of supply is numbered 16. This area is associated with a sulcus lying directly behind the upper end of the arcuate sulcus; this is the sulcus praefrontalis intermedius of Retzius. On the left side (Plate I, fig. 3) there is no detached sulcus in this region but in its place is a well-marked posterior branch of the rectus sulcus. On this side there does not appear at first sight to be a posterior inferior frontal branch; but, on opening up the arcuate sulcus, the artery which is entering its lower extremity is seen to divide at once into two branches; the anterior of these is the middle inferior frontal branch and the posterior the posterior inferior frontal branch. The latter branch supplies the posterior wall of the arcuate sulcus as far as the point at which the posterior limb arises, and then follows this limb and supplies the cortex related to it. Thus the posterior inferior frontal branch on the right side supplies cortex which is lying on the surface; whereas on the left side its area of supply is almost entirely hidden. If we compare this distribution with that in the human brain (Plate IV, fig. 12), the two distributions will be seen to be very similar. The middle inferior frontal branch lies just anterior to a deep sulcus which runs vertically. It passes behind the well-marked inferior frontal sulcus, sending forward branches which supply the posterior part of the inferior frontal gyrus. Above the inferior frontal sulcus the rectus sulcus can be seen with a bifurcated posterior extremity; this extends forwards to the frontal pole. There can be no doubt about this interpretation—if the distribution of the vessels is of any value as a criterion—for the branches of the anterior inferior frontal artery, which have been diverted around the anterior end of the prominent posterior segment of the inferior frontal gyrus, are seen to be limited inferiorly by this sulcus. Furthermore, as we trace the middle inferior frontal branch upwards, branches pass above the posterior end of the rectus sulcus, and the region of the upper end of the arcuate sulcus can be defined. Behind the middle inferior frontal branch the posterior inferior frontal branch can be seen entering the lower end of a sulcus, situated immediately posterior to the lower end of the arcuate sulcus. It is distributed to the anterior part of the gyrus praecentralis, and its area of supply is clearly homologous with the area supplied by the same artery in the Chimpanzee.

The relations of the branches to the island of Reil

In studying and recording the collection of brains in the Collection of the Royal College of Surgeons, Elliot Smith (25) was struck by the fact that in the injected brain of the Chimpanzee D. 666 "the relations of the branches of the middle cerebral artery to the insula and its diminutive opercula are identical with those in the human brain."

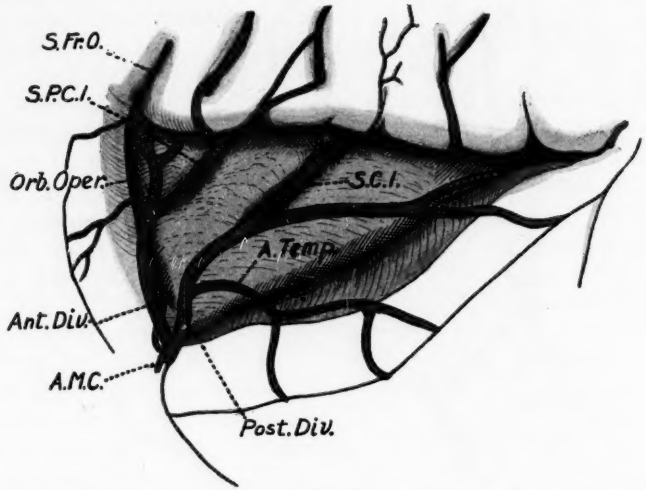


Text-fig. 16. The arteries on the base of the brain of the common Macaque. The distribution of the vessels which emerge from the fissure of Sylvius in higher forms is here shown to be on the orbital surface of the frontal lobe, for the anterior region of the island of Reil is exposed on the surface.

I have been able to confirm this observation in detail not only in the brain of the Chimpanzee, but also in many other anthropoid brains. The resemblance is so striking that at first sight the vessels appear to be exactly homologous; and yet such is not the case, for vessels can only be regarded as homologous when their final areas of supply exactly correspond. There is a variability, but that variability lies within the range of what we might term distributive variability; for example, in the brain of the Chimpanzee on both sides, and in almost every human brain which I have examined, there is an artery running in the sulcus centralis insulae. On the right side in the Chimpanzee this vessel is the parent stem of the anterior and middle central branches and also of the

anterior postcentral branch; on the left side it gives origin to the anterior, middle, and posterior postcentral branches (it will be remembered that on this side the posterior central branch arises from the posterior postcentral branch). The same type of variability is found with the other stem vessels on the island; but it is to be remarked that the component branches emerge from the fissure of Sylvius in corresponding positions on the two sides.

Bearing this type of variability in mind, however, and making allowance for it, these vessels give very valuable information concerning the homologies of the different regions of the insula and the changes which have taken place in the evolution of this region. For example, in the common Macaque (text-

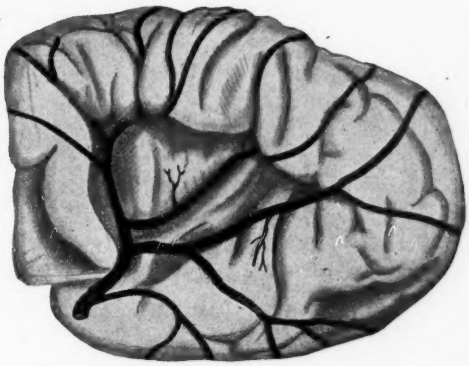


Text-fig. 17. The primary branching of the middle cerebral artery in relation to the island of Reil in the Chimpanzee.

fig. 16) the anterior island of Marchand and the middle island of Holl are exposed on the orbital surface of the hemisphere and the sulcus fronto-orbitalis lies well anteriorly; so also the arteries, which become buried in the higher forms and emerge from the fissure of Sylvius, are here seen spread out on the surface. The arteries give a parallel picture to that seen in the evolution of the opercula.

The middle cerebral artery arises in the usual way from the internal carotid artery. Its course is shown in Plate II, fig. 7 skirting the anterior border of the temporal pole and ending on the small exposed area of the island of Reil corresponding with the anterior island of Marchand. The posterior pyriform artery arises close to its point of origin; the temporo-polar branch midway between its origin and the point at which the lateral striate vessels arise. At the outer border of the pyriform area the main artery breaks up into its

terminal branches. These are generally stated to be four or five in number; in point of fact the numeration of these branches is more or less an arbitrary matter, for the pattern of the primary branching varies. In the brain of the Chimpanzee the main artery divides into two primary divisions on the left side, whereas the main artery on the right side appears to be carried back to the posterior end of the fissure of Sylvius, giving off branches as it goes. All varieties of pattern are seen in the human brain but when they are analysed the differences are far more apparent than real. We will therefore describe here the pattern on the left side of the brain of the Chimpanzee, and compare it with the human brain shown in text-fig. 18.



Text-fig. 18. The primary branching of the middle cerebral artery in relation with the island of Reil in Man.

The middle cerebral artery usually divides into two divisions. The anterior division commences at the outer border of the pyriform area and proceeds laterally to end on the anterior island of Marchand, where it divides into terminal branches. The lateral striate arteries arise close to its point of origin and proceed inwards to the site of the erased endorhinal fissure. Close to the point of origin of these vessels a small artery arises and turns outwards to run in the orbital operculum. This small branch forms the common stem on the left side for the orbital and fronto-marginal branches; on the right side they arise independently. The lateral striate arteries appear to be closely associated with the orbital branch; for I have frequently observed them arising from a common trunk in the Orang and in Man. The lateral striate arteries would therefore seem to be more closely related with the anterior division of the middle cerebral artery; in fact it is not at all unusual to see them arise from an anterior branch rather than from the main vessel. One finds this also in lower forms; in Echidna, Myrmecophaga and numerous members of the Carnivora I have observed it. After giving rise to the lateral striate and first cortical branches, the anterior division passes outwards and divides into four branches.

These are shown in text-fig. 17. The most distal two branches are the two branches of the anterior inferior frontal branch which we have seen leaving the outer end of the fronto-orbital sulcus. These two branches supply area 18. The branch immediately proximal to these passes under the frontal operculum, and, emerging on the surface, enters the lower end of the sulcus arcuatus where it divides into middle and posterior inferior frontal branches. The remaining branch of the anterior division lies in the sulcus praecentralis insulae and, under cover of the fronto-parietal operculum, divides into three branches. These are the anterior central branch to area 15, the middle central branch to area 14 and the small branch to area 13 seen in text-fig. 4.

The inferior division of the middle cerebral artery is related to the temporal operculum. The first branch to arise from it is the temporal branch, which divides before it emerges from the fissure of Sylvius into the anterior and posterior temporal branches to areas 2 and 3. The main division then comes into relation with the sulcus centralis insulae, and here a branch is given off which passes along this sulcus to the parietal operculum. In text-fig. 18, showing the human condition, the artery which lies in this sulcus arises from the anterior division. This is merely a variation in distribution. In the Chimpanzee the artery lying in the sulcus centralis insulae gives rise to the anterior middle and posterior postcentral branches and thus supplies areas 8, 9, 10, 11 and 12; whereas on the right side the artery which lies in this sulcus supplies areas 10, 11, 12, 13, 14 and 15. The continuation of the main stem gives rise to the parietal branches.

The anterior cerebral artery

The branches of the anterior cerebral artery

The branches will be described in the first instance from the points where they emerge from the great longitudinal fissure, after which will be described their relations and distribution on the medial surface.

The frontal branches

The prefrontal branch (Area 22). This branch is commonly known as the internal orbital branch. It is here named in accordance with its area of supply. It arises in this specimen from the fused median anterior cerebral artery. It passes along the inferior border of the hemisphere for a short distance and then divides into medial and lateral branches. The medial branches supply the medial surface as high as the sulcus subrostralis. The lateral branches pass outwards above the olfactory tract and bulb and supply an area as far as the line of demarcation between the middle and anterior cerebral arteries. Anteriorly the area of supply extends as far forward as a transverse sulcus lying at the frontal pole. I have described this artery in Man and in the Orang-utan. The distribution in this specimen corresponds in every particular. Its area of supply almost exactly corresponds with the area praefrontalis of Elliot Smith

and with area 11 of Brodmann. The artery is therefore named the prefrontal branch.

The fronto-polar branch (Area 23). This branch springs from the unpaired artery and is seen to emerge from the great longitudinal fissure at the frontal pole, where its branches are distributed to the cortical area lying in relation to the anterior end of the sulcus rectus. The line of demarcation here corresponds to the line of demarcation between the fronto-marginal and fronto-polar areas of Elliot Smith. Its area of distribution coincides with the fronto-polar area of Elliot Smith.

THE SULCI OF THE SUPERIOR FRONTAL REGION

Before proceeding to the description of the remaining branches of the anterior cerebral artery, it is desirable to discuss the arrangement of the sulci in the superior frontal region. The writer feels that previous attempts to homologise the sulci of the frontal lobe in Man with those of lower forms have proved to be fruitless. This has been due to the fact that the usual diagrammatic representation of the frontal sulci does not conform with the actual appearance of the sulci themselves. To establish homologies individual morphological features must be identified and compared. Such features are very evident in the frontal lobe of such forms as the Macaque; the arcuate and rectus sulci are almost constant in form and position; the superior precentral sulcus is present as a triradiate sulcus. A plea is here put forward to discard the current description of this region of the human brain, founded in the infancy of the science of comparative anatomy; and to attempt to establish certain datum points from which further survey can be carried out. The writer's conception of the evolution of the frontal lobe is founded on the study of the general topographical features of a large series of brains with which the arterial supply has been contrasted. This conception will be dealt with in detail in a separate section of this communication; for the moment the sulci which come into relation with the branches of the anterior cerebral artery will be described.

The superior precentral sulcus in the Chimpanzee is a triradiate sulcus lying immediately anterior to the upper end of the sulcus centralis (Plate II, fig. 5, and text-fig. 6). The two posterior limbs lie parallel with the sulcus centralis and constitute the sulcus praecentralis superior. The anterior limb is directed forwards and is slightly longer on the right side. This sulcus is recognised as a component of the superior frontal sulcus of human anatomy. For the purpose of description it will be here named the element a of the superior frontal sulcus. The identity of this triradiate sulcus in all the anthropoids and in Man cannot be disputed. It occurs as the usual form in the Macaques, Orang, Gorilla and Chimpanzee. Flashman (11) describes it as separate in the brain of the Australian aboriginal, Hrdlicka (16) in the Eskimo brain, Genna (12) in the brain of the Cameroon, and Retzius (19) depicts it in many of his figures.

The superior frontal sulcus is represented in this brain by the element α—the anterior limb of the sulcus praecentralis superior—and by two curved indentations lying anterior to it. These are here named the elements β and λ (Plate IV, fig. 13).

Anterior to the element λ on the right side (Plate IV, fig. 13) there is seen a curved sulcus which extends as far forward as the anterior pole of the hemisphere. This sulcus curves backwards to the centre of the frontal lobe and is recognised as the sulcus rectus. On the left side the anterior end of it appears to be separated off. This separated portion is the homologue of the sulcus fronto-marginalis and is a derivative of the sulcus rectus. These sulci constitute the fundamental sulci of the superior region of the frontal lobe.

The anterior superior frontal branch (Area 24). This vessel branches before it reaches the longitudinal fissure. Its branches are seen entering the anterior end of the sulcus rectus anteriorly; and crossing the element λ of the superior frontal sulcus posteriorly. Its area of supply is thus limited superiorly by the sulcus rectus and encloses the element α within it.

The middle superior frontal branch (Area 25). This vessel emerges from the longitudinal fissure in relationship to the element β of the superior frontal sulcus. On the right side it enters the anterior end of this element and on the left side it crosses it. On both sides its area of supply comes into contact with that of the middle inferior frontal branch of the middle cerebral artery. On the left side branches actually pass into the anterior end of the arcuate sulcus and there enter into anastomotic union with the middle inferior frontal branch. On the right side this anastomosis takes place on the surface of the gyrus separating the element β and the sulcus arcuatus.

The posterior superior frontal branch (Area 26). This is a small branch which is associated with the element α of the superior frontal sulcus and whose area of supply is contiguous with that of the posterior inferior frontal branch of the middle cerebral artery.

The central branches (Area 27)

In text-fig. 6 these branches are shown as supplying three areas, but, whether it is here possible to separate three autonomous areas, could not be determined from the single specimen on account of the asymmetry of the distribution. On the right side (Plate II, fig. 5) an artery is seen crossing the centre of the triradiate sulcus and passing to the posterior border of the sulcus praecentralis intermedius. Behind this an artery divides into two branches; the anterior of which is confined to the region anterior to the central sulcus, whilst the posterior branch crosses the central sulcus to supply its posterior wall in its upper part. It is seen then that the first two are very closely associated with the supply of the centre for leg movements; the third supplies the sensory cortex in its upper part. This is the artery which anastomoses with the anterior postcentral branch of the middle cerebral artery in the human brain (Plate IV, fig. 12).

On the left side also three arteries are seen. The anterior of these is related to the sulcus praecentralis superior, as on the right side; but its area of supply is more extensive; the second branch supplies the anterior wall of the central sulcus in its upper part; whilst the third branch supplies the posterior wall of the same sulcus. Whilst I am of the opinion that these three vessels constitute morphological units, it seems preferable, on account of the importance of their supply to the leg area in cases of occlusion of the anterior cerebral artery, to leave their detailed description for the present.

The parietal branches

The anterior superior parietal branches (Area 28). These branches are related to the curved sulcus in the superior parietal lobule. They arise from a common stem within the sulcus cinguli and emerge from it as three elements. In text-fig. 6 the area supplied by each of these elements is shown. These vessels form the line of demarcation between the anterior and middle cerebral arteries in this region and are contiguous with the middle and posterior postcentral branches and the anterior parietal branch of the middle cerebral artery. In the human brain there are well-marked inosculations between the two major arteries across this line of demarcation.

The posterior superior parietal branches (Area 29). The distribution of the anterior cerebral artery passes backwards into the parieto-occipital fissure. It was not possible to determine its supply in the depths of this fissure, but the artery which passes into it supplies the superior parietal lobule in its posterior part.

The distribution of the anterior cerebral artery on the medial surface of the hemisphere

This distribution is shown in Plates V and VI, figs. 19 and 20. Before proceeding to the description thereof the reader is particularly referred to fig. 8 in my paper on "The Arteries of the Brain of the Orang-utan" (1927 *a*). The significance of the constancy of arterial pattern is clearly shown by the comparison of the figure of the distribution of the arteries in the Orang with the distribution in the Chimpanzee. This comparison is a valuable aid to the study of the homologies of the different parts of the brain.

The anterior cerebral artery springs from the internal carotid artery and passes forwards and inwards to the commencement of the great longitudinal fissure where it joins with its fellow to form a median unpaired artery in this specimen. Thus there is strictly speaking no anterior communicating artery. The unpaired vessel extends for a distance of about an inch to the level of the genu of the corpus callosum, and then divides into two anterior cerebral arteries. The course of these two vessels is the same on both sides. They run over the genu and pass backwards closely applied to the dorsal surface of the corpus callosum, to which they give numerous branches. About one inch

anterior to the splenium the main artery turns upwards and divides into terminal branches. A fine branch, continuing the direction of the main stem, continues to be closely applied to the corpus callosum. This branch turns round the splenium and can be traced as far forwards as the region above the foramen of Munro; its final supply could not be determined.

Branches spring from the anterior cerebral artery in the three parts of its course. The branches from the first part have not been examined in detail, but branches may be seen passing to the trigonum olfactorium and to the paraterminal body. On the right side the recurrent branch, or Heubner's artery, springs from the first part of the artery just before it fuses with its fellow. This vessel passes outwards to the site at which the lateral striate arteries pass to the erased endorhinal fissure, and enter a row of perforations anterior to those formed by the lateral striate branches of the middle cerebral artery. The recurrent branch sends branches to the olfactory tract which can be traced almost as far as the bulb on both sides. The olfactory bulb is usually described as being supplied by the medial orbital cortical branch, but I have never seen any evidence of such a supply. On the left side the recurrent branch springs from the first cortical branch of the medium unpaired vessel. No cortical branches spring from the first part of the artery. The arrangement of the recurrent branch of the anterior cerebral artery is well shown in text-fig. 16 showing the arteries in the common Macaque. This arrangement is in exact agreement with my previous description of these vessels in Man (1920), and with the drawings of Aitken (1).

The branches of the median anterior cerebral artery

Two branches spring from this part of the artery. The first is the prefrontal branch to area 22. It is seen in Plate V, fig. 19 passing downwards to reach the orbital surface on the right side; in Plate VI, fig. 20, showing the distribution on the left side, this branch also gives off the fronto-polar branch which enters the fronto-marginal sulcus. This branch springs from the second branch on the right side. This arrangement provides a very good example of a difference in distribution. The second branch is the anterior superior frontal branch to area 24. It is seen to divide into two branches on the medial surface; the posterior of these is the vessel related to the element λ of the superior frontal sulcus.

The branches of the third part of the anterior cerebral artery

The middle superior frontal branch. This vessel arises at the level of the genu on both sides, crosses the sulcus cinguli and proceeds to the area 25 as described above.

The posterior superior frontal branch. On the right side this vessel arises independently and proceeds to area 26; on the left side it arises from the most anterior of the central branches.

The central branches

On the right side a common stem gives origin to the three branches, grouped together as the central branches. On the left side the anterior one has been seen to arise in common with the posterior superior frontal branch, the other two arising from a common stem.

After these branches are given off the artery leaves the corpus callosum and passes into the sulcus cinguli. Here it divides so as to send a large vessel to the end of that sulcus to emerge on the superior parietal lobule, and one large branch which passes backwards to the parieto-occipital fissure.

No attempt has here been made to subdivide the areas on the medial surface.

The posterior cerebral artery

The distribution of this artery has already been fully discussed by me in the brain of the Orang-utan and in Man (1927 *a*, *b*); and since the distribution is so similar in this specimen no further description is here necessary beyond that of the supply of the striate cortex which will be dealt with in the next section.

GENERAL DISCUSSION AND SUMMARY

Three questions of interest stand out clearly in this investigation and will be discussed in this section. They are, firstly, the extent of anastomoses and their sites; secondly, the extent of the encroachment on the occipital operculum of the supply of the middle cerebral artery; and thirdly, the value of the distribution of the arteries in determining homologies with particular reference to the frontal lobe.

The anastomosis of cortical arteries

The problem of the extent of the anastomoses between the cortical arteries is one which cannot be said to have been satisfactorily solved. Heubner (14) described an anastomotic network in the pia mater through which the blood may be drawn from neighbouring areas. His papers are not available to me and references to his work are taken from Charcot and Beevor. Charcot disputes Heubner's opinion and holds that Duret's opinion is correct that, although anastomoses do exist, they take place through vessels of fine calibre, but not in the pia mater. Now in the writings of Charcot I can find no evidence that any distinction was made between anastomoses which may occur between the contiguous branches of either of the three major arteries, and anastomoses which may occur at the terminal line of demarcation between the three major arteries. This distinction is very important, and more particularly from the clinical point of view; and here my own observations, although not altogether suitable for the determination of finer types of anastomoses, are more in harmony with those of Beevor who recognised this distinction. His observations are so important that a somewhat full quotation from his work is here warranted.

Duret states that he has never found an anastomotic network in the pia mater, although Heubner and other anatomists described such a network (*Kanalnetzwerk*). To determine this question, I have made the following experiment. The third branch of the middle cerebral artery, viz. the ascending parietal branch, was ligatured close to the Sylvian fissure, and the anterior, middle and posterior cerebrals were then simultaneously injected after cutting out the posterior communicating artery. It was found on subsequently cutting the hardened brain horizontally that the convolution supplied by this ascending parietal branch were injected by the coloured gelatine from the anterior cerebral artery. This would show that either there is no communication between the contiguous branches of the middle cerebral artery, or that the communication is so slight that it is easier for the blood to reach the area corresponding to the ligatured artery from the branches of the anterior cerebral artery than from the contiguous branch of the same artery, or, in other words, that the communication between the middle cerebral artery and the anterior cerebral artery, where their areas touch, is much more free than that between the contiguous branches themselves of the middle cerebral artery.

The whole of Beevor's observations are made from the examination of the extent to which the vessels were injected by the colouring matter which he used. His experiment indicates that vessels of considerable calibre are probably present along the line of demarcation of the supply of the three major arteries. Duret found that anastomosis took place between vessels of fine calibre; and for this reason Charcot brings Heubner's observations into dispute. Charcot says:

"Heubner maintains that the communications in question are very free, and that they take place through the medium of vessels which are not less than a millimetre in diameter."

Now a channel of not less than a millimetre in diameter is relatively large in this region; and of a size which would be in accord with the results of Beevor's experiment. Furthermore in support of such vessels Charcot is bound to admit that:

"pathological cases occur in which obstruction of one of the vessels of the cortical system, or of its branches, has not revealed itself during life by any evident symptom, and in which death, having supervened, the cerebral pulp has not presented at the autopsy, in the parts corresponding to the obstruction, any trace of softening."

In this communication these large anastomosing channels have been seen in many places. In the human brain they are found along the line of the inferior temporal sulcus, on the surface of the superior parietal lobule, around the preoccipital region, on the surface of the postcentral gyrus and in the superior frontal region. In places where a cortical area of the same histological structure passes from one vascular area to another, anastomotic vessels occur. This I have observed in the preoccipital region, in the area of the sensory cortex, and at the point where area 6 of Brodmann runs across the vascular line of demarcation. My observations, however, on this subject are not yet

extensive enough to warrant a definite conclusion as to the exact sites and the constancy of position of these channels connecting the areas of the three main vessels.

Their presence is undoubtedly the reason for the slight effects of arterial occlusion in some cases; and so it is very desirable to determine their exact positions and constancy, or otherwise, of arrangement.

Beevor obviously recognised their existence and so it is strange that he did not take them into consideration in determining the line of demarcation of the supply of the three major arteries. I have found this line of demarcation to be so constant that it is of value in identifying sulci and other structures; and yet Beevor's figures show such variation that our results appear to be inconsistent. This is the more remarkable when it is considered that my injections of the basal regions of the brain confirm his observations to the smallest detail, e.g. the anterior nucleus of the thalamus standing out as an island and the anterior commissure forming the line of demarcation between five different arteries. The differences in our observations in the cortical regions are due to the fact that I have found the line of demarcation from the dissection of the vessels, whereas the line of demarcation found by Beevor is not a vascular line but a colour line.

It is apparent that, since there is little if any anastomosis between contiguous branches, the freedom of the anastomosis along the line of demarcation precludes the use of the method of differential injection for the investigation of the cortical supply, unless it is fully confirmed by dissection. For this reason Beevor's fig. 6 cannot be accepted as a correct analysis of the minimal and maximal distribution of the middle cerebral artery.

But in thus contending that the line of demarcation as determined by dissection is more accurate than when determined by the method of differential injection, there are admitted difficulties which we may here discuss. In the case of end arteries the line of demarcation is obviously easy to determine at the capillary line of junction; but in the case of the cerebral cortex, which, taken as a whole, might be regarded as a morphological unit of structure, consisting of secondary departments, the arteries are not end arteries. Between contiguous branches the line of demarcation appears to be similar to that between end arteries; but between the major arteries themselves definite communications exist. The line then between the major arteries is not necessarily avascular, and this together with the depth at which the arteries lie in the sulci makes the determination difficult. In those places where the major vessels are connected by anastomoses of considerable size the selection of the point in the anastomotic channel which is to be regarded as on the line of demarcation is an anatomical and not necessarily a physiological consideration. Fortunately the anatomical selection is rendered easy when the anastomotic channel lies on the surface of a convolution (as at the point marked by an asterisk in Plate I, fig. 1), for the neutral point is indicated by the angles at which the branches are given off on either side of it. Those branches which are given off from the anterior cerebral side are directed towards the middle

cerebral area and *vice versa*. This observation is confirmed at the sites of anastomosis shown in Plates III and IV, figs. 11 and 12.

The presence of these anastomotic channels however makes it possible that the actual physiological line of demarcation may vary from time to time; and that Beevor's maximal and minimal areas of distribution may be physiological rather than anatomical limits. This is not necessarily so, however, for the path of least resistance in the differential injection is not determined by physiological demands, but by purely physical conditions, determined by the amount of blood clot left in the vessels and whether this clot lies in vessels which themselves lie in the depths of the sulci.

Temple Fay (10) made use of a radiographic method to throw light on these problems. His conclusions bear out mine in many particulars. He found that well-defined arterial trunks directly connected the anterior, middle and posterior cerebral arteries. He further makes the interesting observation that:

"Cortical end arteries do exist to a large extent and particularly in the fields of each arterial supply, the points of fusion between the three main systems being characterised by anastomotic branches."

Thus his observations so far are in entire accord with the results obtained by pure dissection. He, however, was able to carry his observations beyond those possible by dissection; and records the presence of subcortical arterial loops within the area of distribution of the anterior cerebral artery.

He further describes an avascular zone extending from the frontal lobe to the parietal region. This avascular region agrees closely with the line of demarcation between the anterior and middle cerebral arteries. On account of the surgical importance which he attaches to it, it is necessary to point out the extent to which my own observations are in disagreement with his. He states that "should a transcortical approach to the deep structures of the brains or ventricle be required, there is relatively no danger of encountering large vessels, which might cause awkward bleeding or impair a definite area from circulation by ligation or rupture." Across the line of demarcation I have already described the anastomotic vessels as channels indicating their relatively large size and Fay agrees in so far as he names them arterial trunks. The branches of the anterior cerebral artery as shown in Plate IV, fig. 13, are large and the line of demarcation is found at the bottom of the sulci in many places; so that, if incision is made at the avascular zone so-called, the incision would have to be made through the bottom of the sulci, causing injury to the vessels on either wall; if the incision is to be made medial or lateral to the line it would encounter the large vessels passing to the line of demarcation. In any case injury might well be made to the anastomotic channels; but in this case collateral circulation would be established. Another point which must be taken into consideration in choosing a site for transcortical approach is the venous distribution; and it is across the line indicated by Fay that the veins are reaching their maximum size before entry into the longitudinal sinus.

Unfortunately I have no facilities for the radiographic examination of injected brains, so I wish particularly to call attention to the importance of Fay's paper which has only recently come to my notice.

The arterial supply of the striate or visual cortex

In the brain of the Chinese, described by me (1927 *b*), the area of supply of the calcarine branches of the posterior cerebral artery exactly corresponded in extent with the area of the striate cortex; and in that specimen the lunate sulcus formed the boundary of the arterial and cortical areas. Further, the arterial supply, having been determined by differential injection, was confirmed by the dissection of the vessels themselves. In the study of the arteries of the brain of the Orang-utan (1927 *a*), it was pointed out that the extreme edge of the lunate operculum was invaded by the anterior and middle cerebral arteries. In the Orang this edge was narrow and did not detract from regarding the striate cortex as an autonomous vascular area. In the brain of the Chimpanzee, here described, the width of this border supplied by the anterior and middle cerebral arteries (area 4) is more extensive; and, moreover, one cannot make light of the fact that the superior occipital sulcus lies within the middle cerebral area anteriorly. Ariens Kappers (1926) shows in numerous figures that the preoccipital area encroaches for some distance on the surface of the operculum in various forms; but in all these figures the superior occipital sulcus is depicted as lying within the area striata. It would appear therefore that in the Chimpanzee the area striata is supplied in its anterior part to a slight extent by the middle cerebral artery.

Further observations have been carried out on the human brain to ascertain whether the middle cerebral artery encroaches on the striate area. The supply of the calcarine branch of the posterior cerebral artery is limited to the striate cortex in a great number of specimens and in many others the anterior edge is supplied by the middle cerebral artery. In Plate VI, fig. 21, the posterior region of the brain which is depicted in Plates III and IV, figs. 11 and 12, is drawn to show the relationships. On both sides there is a well-marked sulcus lunatus. On the left side the calcarine branches are seen emerging from both lips of the superior occipital sulcus; branches of the middle cerebral artery pass on to the surface of the operculum from the anterior aspect, and the line of demarcation between these branches and those seen emerging from the superior occipital sulcus is marked by a shallow depression. Two cuts were then made at right angles to one another to demonstrate the line of Gennari. The horizontal cut was made on the level of the superior occipital sulcus and showed an exact coincidence of the arterial supply with the extent of the striate cortex in that direction. The vertical cut passed through the shallow depression at the vascular line of demarcation and showed that the line of Gennari likewise stopped at this depression. On the left side therefore the calcarine supply and the line of Gennari were coincident; and the specimen confirmed my previous observations (1927 *b*). On the right side two cuts were

made in a similar way. The horizontal cut (Plate VI, fig. 21) showed exact coincidence; the vertical cut, however, showed that the striate cortex extended into the middle cerebral area for a distance of a quarter of an inch. This is indicated in the figure by shading. There was no evidence of any anastomosis between the two systems.

It is therefore apparent that, whilst the calcarine artery might well be termed the artery of the striate cortex, the striate cortex is sometimes supplied in its anterior part by the middle cerebral artery. The extent to which this takes place is the subject of further observation.

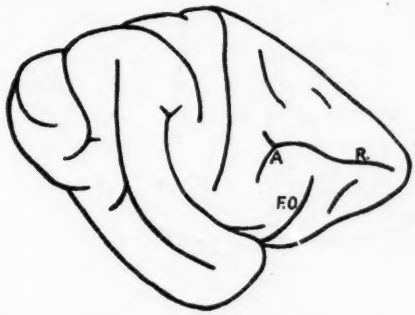
The sulcal pattern of the frontal lobe

In determining the homologies of the sulci of the brain it is important to consider every fact which may bear on the question. Variation in cortical pattern, differences in shape and continuity of sulci and other factors make the problem a difficult one. In discussing the evolution of the parallel sulcus (1927 *c*) the criteria to be established before homology could be regarded as certain, were stated to be the general form of the sulcus, its relationship with neighbouring sulci, its association with cortical areas and its phylogenetic and ontogenetic development. To these were added the relation of blood supply to cortical structures. In this section it is intended to illustrate how this criterion is used; but it must be emphasised that this criterion by itself cannot be regarded as a final one.

Some four years ago the writer was engaged in the attempt to follow out the evolutionary changes which resulted in the evolution of the frontal lobe from the simple arcuate rectus pattern of lower forms to the more complex pattern seen in many of the Orang specimens. With the increased light which is thrown on the problem by the arterial supply it seems possible to trace these changes sufficiently to warrant discussion.

The frontal lobe in the Circopithecidae shows the rectus arcuate complex as two simple sulci. The rectus sulcus is a straight sulcus which passes posteriorly into the concavity formed by the arcuate sulcus (Plate V, fig. 14). At this stage the lateral border of the hemisphere is curved and lies more or less parallel with the arcuate sulcus. Into this curved lateral border the sulcus fronto-orbitalis impresses itself. In some forms, however, this sulcus is rudimentary and is confined to the orbital surface; but in these cases the highest point of the concavity of the lateral border of the hemisphere is in line with the outer end of the sulcus fronto-orbitalis. In the Gibbon the rectus arcuate complex consists of a single curved sulcus of quite characteristic form (text-fig. 22). This curved sulcus consists in reality of the two sulci; for on opening up the horizontal arm the rectus sulcus can be distinguished on the superior wall. Within the concavity of the sulcus, and cutting into the lateral margin of the hemisphere, there is a more distinct sulcus fronto-orbitalis than that seen in the Circopithecidae. The Gibbon also shows a more advanced condition of the infolding of the island of Reil. Immediately posterior to the

sulcus fronto-orbitalis a horizontal sulcus is seen passing out from the fissure of Sylvius, and lying immediately below the posterior end of the arcuate sulcus. This sulcus is produced by the folding of that area of cortex which Anthony (2) names the gyrus reuniens. This horizontal sulcus, according to Anthony, lies anterior to the old suprasylvian sulcus, which is already buried in the island, and constitutes his sulcus posterior transversus gyri reunientis. In the Macaque the gyrus reuniens lies anterior to the temporal pole and on the surface of the orbital region; in other words, the anterior island of Marchand and the middle island of Holl are both exposed and lie posterior to the sulcus fronto-orbitalis (text-fig. 16). In the Gibbon the infolding of the middle island of Holl is indicated by the presence of the sulcus posterior transversus gyri reunientis. In the Orang and in the Chimpanzee this folding has progressed further so that the sulcus fronto-orbitalis is now represented by the deep opercular sulcus of the orbital operculum: the superior limiting sulcus of the island of

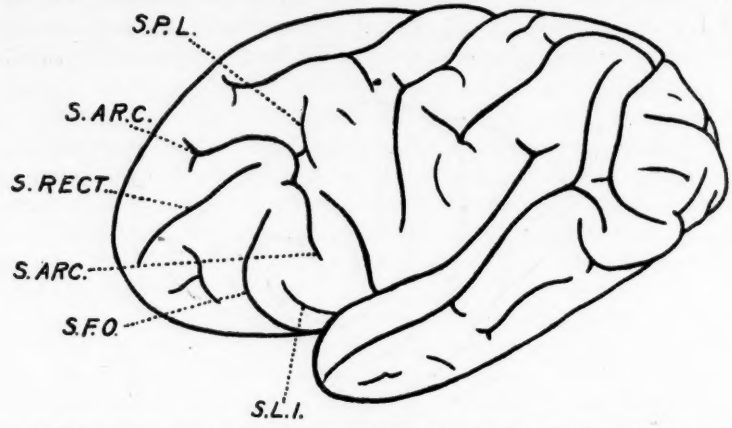


Text-fig. 22. The brain of the Gibbon to show the form of the arcuate rectus sulcus (*A.R.*).

Reil has extended forward and deepened so as to form and include anteriorly the sulcus anterior transversus gyri reunientis. The middle island of Holl is now completely buried and the anterior island of Marchand is only visible on the surface between the frontal and temporal opercula. For a fuller understanding of the forward encroachment of the frontal lobe by the development of the opercula the reader is referred to Anthony's papers, and particularly to his paper "Le Développement du Cerveau chez les Singes."

If the secondary branches of the middle cerebral artery are capable of being homologised in the various members of the Primates, it is clear that in the lower forms these vessels will be found exposed on the orbital surface of the operculum, and in the higher forms the vessels will have become folded into the island with the infolding of the gyrus reuniens and the anterior regions of the island. We have seen that the arteries show these stages as clearly as do the other morphological structures. In the Chimpanzee the anterior inferior frontal branch of the middle cerebral artery emerges from the outer end of the sulcus fronto-orbitalis to supply area 18, limited superiorly by the sulcus

rectus. In the Macaque (Plate IV, fig. 12) all the branches, which were named frontal branches in the general description, lie exposed on the orbital surface of the frontal lobe. Of those branches which pass over the lateral border of the hemisphere, the most anterior lies on the outer end of the sulcus fronto-orbitalis. This artery is limited in its supply superiorly by the sulcus rectus. Its distribution has been seen in the brain of *Circopithecus mona*. The next branch is the middle inferior frontal branch which is related to area 8 of Brodmann; and behind this are seen the posterior inferior frontal and anterior central branches. The arteries which have been described as the branches of the anterior division of the middle cerebral artery in the Chimpanzee are all recognised in the Macaque and furthermore their relationships

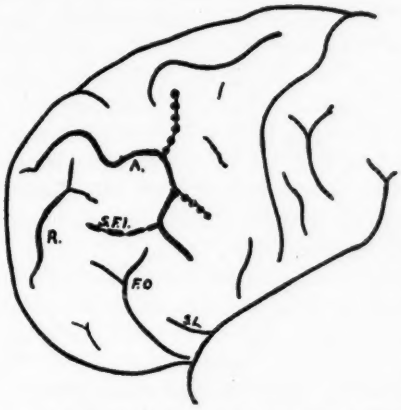


Text-fig. 23. The left hemisphere of the brain of the Orang to show the pattern of the arcuate and rectus sulci.

to the areas on the orbital surface are in exact correspondence with those areas of the cortex—the anterior island of Marchand and the middle island of Holl—which have been shown to have been folded into the island of Reil (Plate V, fig. 14 and text-fig. 16).

In the Chimpanzee the sulcus rectus is seen to be a curved sulcus extending well forward to the frontal pole; posteriorly it is separated from the arcuate sulcus by a narrow gyrus. The arcuate sulcus (text-fig. 2) passes above the posterior end of the rectus sulcus. A reference to Plate V, fig. 14 and text-fig. 15, in which the arterial supply is contrasted with the cortical pattern, makes it certain that the upper end of the arcuate sulcus will be found above the posterior end of the rectus sulcus in higher forms. The arterial supply of the brain of the Chimpanzee fulfils these expectations. Text-figs. 23 and 24 were taken from brains of Orang. In text-fig. 23 is shown a specimen in which the primitive arrangement is retained. Behind the arcuate sulcus the sulcus praecentralis intermedius has almost separated from the arcuate sulcus. In text-fig. 24 the

arcuate sulcus is more complex; for the sulcus praecentralis intermedius is still joined to the arcuate sulcus and in addition we see a compensatory sulcus passing forward from the anterior wall of the arcuate sulcus. This compensatory sulcus lies below the posterior end of the rectus sulcus and agrees in position with the sulcus seen in Plate I, fig. 3. I have named it the sulcus frontalis inferior. The posterior relations of the rectus sulcus take a fairly constant position lying in the curve of the arcuate sulcus. Anteriorly its relations are very constant. It extends forwards to the frontal pole. Pictures taken from the anterior aspect (text-fig. 10 and Plate IV, fig. 13) show it to extend into the rostrated frontal pole in the Chimpanzee and in the Orang. The human pattern can only be determined by carefully defining fixed datum points in terms of



Text-fig. 24. The frontal lobe of the brain of the Orang (No. 1).

primitive sulci in the same manner as the morphology of the occipital region was determined by Elliot Smith. In the frontal lobe these datum points for primitive forms are as follows: the anterior and posterior ends of the arcuate sulcus, the anterior and posterior ends of the rectus sulcus, the outer end of the sulcus fronto-orbitalis, the two sulci transversi gyri reunientis and the temporal pole.

The temporal pole of the hemisphere is included, for its forward extension, as evolution proceeds, gives a valuable clue to the positions where growth has taken place. In the Circopithecidae the general picture of the frontal lobe is that of a triangle bounded by the sulcus centralis posteriorly, the superior border of the hemisphere superiorly and the inferior border of the hemisphere inferiorly. It is to be noted that the fissure of Sylvius enters into this border posteriorly; and as evolution proceeds this fissure enters more and more into the constitution of this boundary. Within the major triangle lies a second triangle whose boundaries form the basis of this analysis. This triangle is bounded antero-superiorly by the sulcus rectus, posteriorly by the lower half of the arcuate

sulcus and inferiorly by the inferior border of the hemisphere lying between the anterior end of the rectus sulcus and the inferior end of the arcuate sulcus. In the Circopithecidae this inferior boundary lies wholly in front of the temporal pole; whereas in the higher anthropoids the inclusion of the anterior island of Marchand into the island of Reil brings the fissure of Sylvius into its constitution. The apex of the triangle lies between the rectus and arcuate sulcus and is open. Text-fig. 15 shows that Brodmann's area 8 appears to flow through the open apex of the triangle.

The arteries bear a constant relationship to the different elements of this smaller triangle in all forms; and by carefully tracing these arteries the homologies can be established. The anterior end of the sulcus rectus retains its position in relation to the frontal pole and the cortex surrounding it is supplied by the fronto-marginal branch of the middle cerebral artery in the Chimpanzee and in Man. In Plate IV, fig. 13 the anterior end of the rectus sulcus is seen to be detached on the left side. On the right side the sulcus rectus is complete. The posterior end of the rectus sulcus forms the posterior limit of the supply of the anterior inferior frontal artery. Now looking at the area of supply of these two vessels in the human brain (Plate IV, fig. 12) the rectus sulcus reveals itself. Its anterior end lies at the frontal pole and is bifurcated. It is related to the fronto-polar branch of the anterior cerebral artery and to the fronto-marginal branch of the middle cerebral artery.

The sulcus commonly called the sulcus fronto-marginalis is then clearly the anterior end of the rectus sulcus; in some cases it is separate as on the left side of the brain of the Chimpanzee. Now in further examining Plate IV, fig. 12, the continuation of the rectus sulcus from the anterior end is seen to correspond with the anterior end of the superior frontal sulcus. This segment of the superior frontal sulcus is here named the element δ, in order to facilitate comparisons. It is quite common to find this element δ or the anterior part of the rectus sulcus, entirely distinct from the superior frontal sulcus. The posterior half of the rectus sulcus then passes obliquely away from the line of the superior frontal sulcus and passes into the middle frontal gyrus so-called. It ends above the inferior frontal sulcus, its posterior end being frequently bifurcated. These relations are well seen in Plate IV, fig. 12. The anterior inferior frontal artery is limited by the rectus sulcus in diagrammatic fashion in this specimen. It is to be particularly noted also in this brain that the growth of the hemisphere, which has taken place more particularly along the base of the triangle, has produced a well-marked inferior frontal sulcus and a prominent Broca's convolution. The branches of the anterior inferior frontal artery do not pass across this convolution. The distribution of the arteries shows clearly how the growth of the hemisphere has taken place immediately anterior to the lower part of the arcuate sulcus. This growth has produced the great infolding of the island in the human brain, the deepening of the sulci transversi gyri reunientis, and the formation of the new compensatory sulcus frontalis inferior. At the same time the posterior half of the base of the smaller triangle has entered

into the formation of the fissure of Sylvius, so that the arteries which were lying on the surface of the orbital region in the Circopithecidae are now bunched together and emerge from the region of the anterior island of Reil.

A further result of the expansion of the cortex which has produced Broca's convolution is seen in the thrusting upwards of the areas 8 and 9 of Brodmann, and in the change in form of area 6; for in the Circopithecidae this area follows the curve of the arcuate sulcus, whereas in man this area, which has started to assume a more vertical position in the Chimpanzee, lies vertically up the hemisphere immediately in front of the Rolandic area. The changes in the direction and form of the arcuate sulcus produced by the growth of the postero-inferior angle of the frontal lobe have hitherto prevented the homology of this sulcus from being established. The arterial supply however reveals the sulcus in the majority of human brains. Its lower end can generally be recognised by the fact that it forms the posterior boundary of Broca's convolution. In the majority of cases it appears to be homologous with the sulcus praecentralis inferior; but here caution is necessary, for associated with this sulcus posteriorly is the posterior inferior frontal branch of the middle cerebral artery, and one frequently sees a sulcus lying posterior to the arcuate into which this branch passes (Plate IV, fig. 12).

The origin of the sulcus praecentralis intermedius is quite apparent. In the Gibbon there is almost constantly present a posteriorly directed branch from the convexity of the curve of the arcuate sulcus; in some specimens the posterior end of this branch is bifurcated. In the Chimpanzee this sulcus is associated with the posterior inferior frontal branch of the middle cerebral artery. On the right side it has become detached from the arcuate sulcus. There is no need to discuss the morphology of this sulcus further, for it has been described by Retzius and others. This sulcus frequently joins the sulcus praecentralis superior, and if at the same time it remains attached to the arcuate sulcus a continuous sulcus runs from the lower end of the arcuate to the upper end of the sulcus praecentralis superior. This continuous sulcus, composed of three definite elements, corresponds with the diagrammatic representation of the sulcus praecentralis of human anatomy.

The upper end of the arcuate can generally be recognised in the human brain by the vascular relations. In Plate IV, fig. 12 it is seen with a bifurcated extremity interlocking with the posterior end of the rectus. In Plate III, fig. 11 it is not bifurcated, but is easily recognised by its relations with the rectus sulcus and with the line of demarcation between the anterior and middle cerebral arteries. Its connection with the superior frontal sulcus will be discussed with that sulcus.

The superior frontal sulcus is composed of four elements. These have already been described as firstly, the anterior limb of the triradiate sulcus praecentralis superior of lower forms, secondly and thirdly the elements β and λ, which are separate elements in lower forms and tend to be conjoined in man, and fourthly the anterior half of the sulcus rectus.

These elements join in different ways so that all forms are seen. In many brains the sulcus praecentralis is separate from the sulcus frontalis superior. Again elements β and λ may join without being connected with the anterior half of the rectus sulcus; and other combinations of the four elements are seen. Perhaps the commonest condition is found in the joining of the sulcus praecentralis superior with elements β and λ. Cole (1911), in describing the brains of three Chinese, came to conclusions regarding the homology of the arcuate sulcus very similar to those put forward in this paper. In his determination of homology he was guided by the cortical pattern and was led to the conclusion that the upper part of the arcuate sulcus is represented in the superior frontal sulcus. In many brains which I have examined the sulcus which has been called the arcuate sulcus is undoubtedly fused with the element β of the superior frontal sulcus. This is however rather an accidental circumstance, or perhaps it would be better to say that the presence of a superior frontal sulcus is accidental. There is a tendency, in other words, towards a folding of the cortex in the superior region of the frontal lobe; and, whilst this folding most frequently takes place along the line of the primitive elements seen in the Chimpanzee, it may take place at a somewhat lower place and so come to include the upper part of the arcuate sulcus. The foldings in this region are in great part compensatory in nature and so there is a great divergency in pattern. This is likewise seen in the region of the inferior frontal gyrus; for here we see in many cases a well formed, almost operculated, sulcus frontalis inferior, and in other cases merely a series of fragmentary sulci, of which the most anterior is sometimes named the sulcus radiatus. The almost universal presence of recognisable arcuate and rectus sulci simplifies the general description of this area. The presence of three parallel tiers named the superior, middle and inferior frontal gyri may be useful for the purpose of localisation; but are not in accord with the morphological features. These features are vertical rather than horizontal.

ACKNOWLEDGEMENTS

Prof. Elliot Smith presented me with the brain of the Chimpanzee which forms the basis of this description. For this and for all the kindness which I have received at his hands I here express my thanks.

For some years I have been receiving specimens of Orang, Gibbon, Macaque and other brains from Mr Boden Kloss and Mr Chasen of Raffles Museum, Singapore. For all the help which they have given me I am very grateful.

For letting me have extracts from papers by Anthony I have to thank Prof. Burkitt of Sydney; and for calling my attention to Fay's valuable contribution I am indebted to Prof. Ariens Kappers.

There are many papers which I should like to have consulted; but they are not available to me in Hong Kong. If therefore the absence of any discussion on the work of Foix, Masson and others (see note in my papers in *Brain*, 1927 *b* (22)) is noted, it will be recognised as not being due to neglect.

ABBREVIATIONS

Anterior Cerebral Artery

A.Ant.Cer.	Anterior cerebral artery.
A.A.S.F.	Anterior superior frontal branch.
A.Cent.	Central branch.
A.F.P.	Fronto-polar branch.
A.M.S.F.	Middle superior frontal branch.
A.Praef.	Praefrontal branch.
A.P.S.F.	Posterior superior frontal branch.
A.Rec.Ant.Cer.	Recurrent branch.

Middle Cerebral Artery

A.A.C.	Anterior central branch.
A.A.I.F.	Anterior inferior frontal branch.
A.A.P.	Anterior parietal branch.
A.A.Pc.	Anterior postcentral branch.
A.A.T.	Anterior temporal branch.
A.F.M.	Fronto-marginal branch.
A.M.C.	Middle central branch.
A.M.I.F.	Middle inferior frontal branch.
A.M.P.	Middle parietal branch.
A.M.Pc.	Middle postcentral branch.
A.Orb.	Orbital branch.
A.P.C.	Posterior central branch.
A.P.I.F.	Posterior inferior frontal branch.
A.P.P.	Posterior parietal branch.
A.P.Pc.	Posterior postcentral branch.
A.P.Pyr.	Posterior pyriform branch.
A.P.T.	Posterior temporal branch.
A.Temp.	Temporal branch.
A.T.P.	Temporo-polar branch.

Posterior Cerebral Artery

A.Calc.	Calcarine branch.

Sulci

S.Arc.	Arcuate sulcus.
S.Cent.	Sulcus centralis.
S.Cent.Ins.	Sulcus centralis insulae.
S.F.I.	Sulcus frontalis inferior.
S.Fr.O.	Sulcus fronto-orbitalis.
S.Li.In.	Sulcus limitans insulae.
S.Lun.	Sulcus lunatus.
S.Mid.Temp.	Middle temporal sulcus.
S.Par.	Parallel sulcus.
S.Praec.Ins.	Sulcus praecentralis insulae.
S.Praec.Int.	Sulcus praecentralis intermedius.
S.Rect.	Sulcus rectus.
S.Sup.Occ.	Sulcus occipitalis superior (sulcus calcarinus lateralis).
Str.Cort.(p.c.)	Striate cortex supplied by posterior cerebral artery.
Str.Cort.(m.c.)	Striate cortex supplied by middle cerebral artery.

DESCRIPTION OF PLATES

PLATE I

Fig. 1. The distribution of the middle cerebral artery on the lateral surface of the right hemisphere in the Chimpanzee.

Fig. 3. The distribution of the middle cerebral artery on the lateral surface of the left hemisphere of the brain of the Chimpanzee.

PLATE II

Fig. 5. The arteries of the dorsal surface of the brain of the Chimpanzee.

Fig. 7. The arteries on the ventral aspect of the brain of the Chimpanzee.

PLATE III

Fig. 9. The arteries of the occipital region in the brain of the Chimpanzee. The symmetrical arrangement of the arteries related to the sulcus occipitalis superior, and the extent to which the middle cerebral artery encroaches on the occipital operculum are to be noted.

Fig. 11. The distribution of the middle cerebral on the lateral surface of the right hemisphere in the human (Chinese) brain.

PLATE IV

Fig. 12. The distribution of the middle cerebral artery on the left side of the brain shown in fig. 11. The asterisks show the position where anastomoses were found between the major arteries. This figure also shows how the arteries are of value in determining the homologies of the arcuate and rectus sulci (see text).

Fig. 13. The brain of the Chimpanzee seen from the anterior aspect to show the relations of the rectus sulcus, the distribution of the anterior cerebral artery and the composition of the superior frontal sulcus so-called.

PLATE V

Fig. 14. The brain of *Circopithecus mona* to show the relations of the arteries to the arcuate and rectus sulci. Compare with text-fig. 15.

Fig. 19. The distribution of the anterior cerebral artery on the medial surface of the right hemisphere of the brain of the Chimpanzee.

PLATE VI

Fig. 20. The distribution of the anterior cerebral artery on the medial surface of the left hemisphere of the brain of the Chimpanzee.

Fig. 21. The posterior view of the brain seen in Plates III and IV, figs. 11 and 12. The coincidence of the supply of the calcarine artery with the extent of the line of Gennari is exact on the left side; whereas on the right side the extent of middle cerebral overlap is shown by the denser shading.

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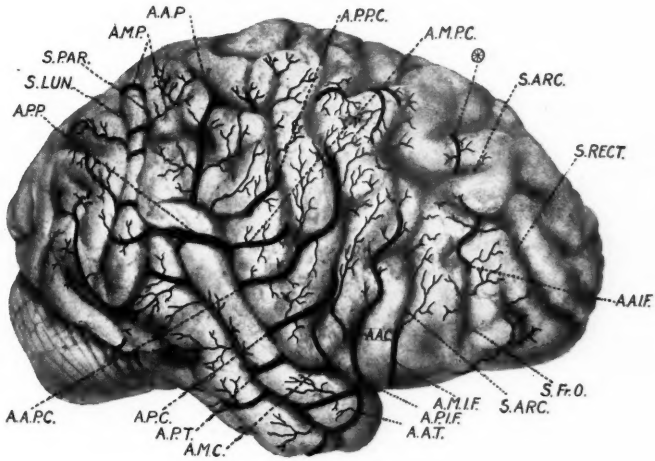
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A.M.P.C.
S.PAR.
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S.ARC.
A.P.P.
S.RECT.
A.A.I.F.
A.A.C.
S.Fr.O.
A.M.I.F.
S.ARC.
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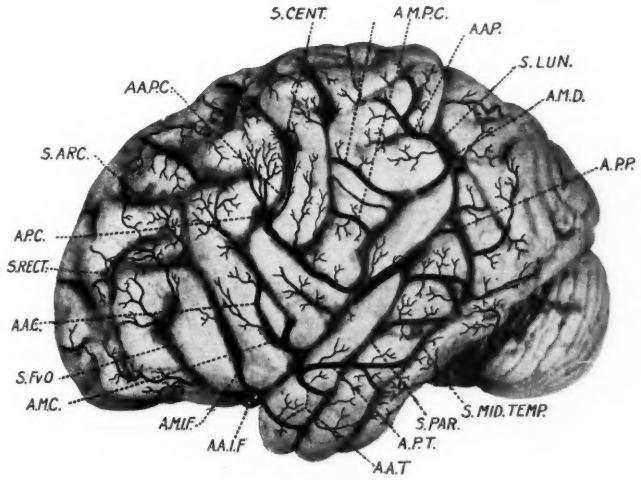
A.M.C.

Fig. 1


S.CENT.
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S.RECT.
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S.Fr.O.
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Fig. 3

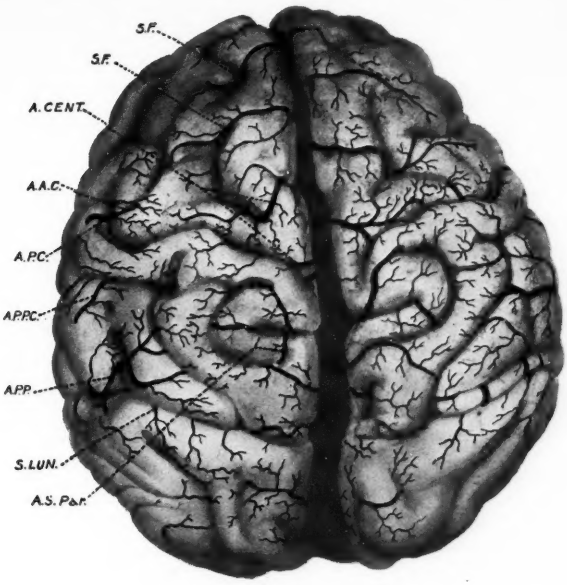

Fig. 5

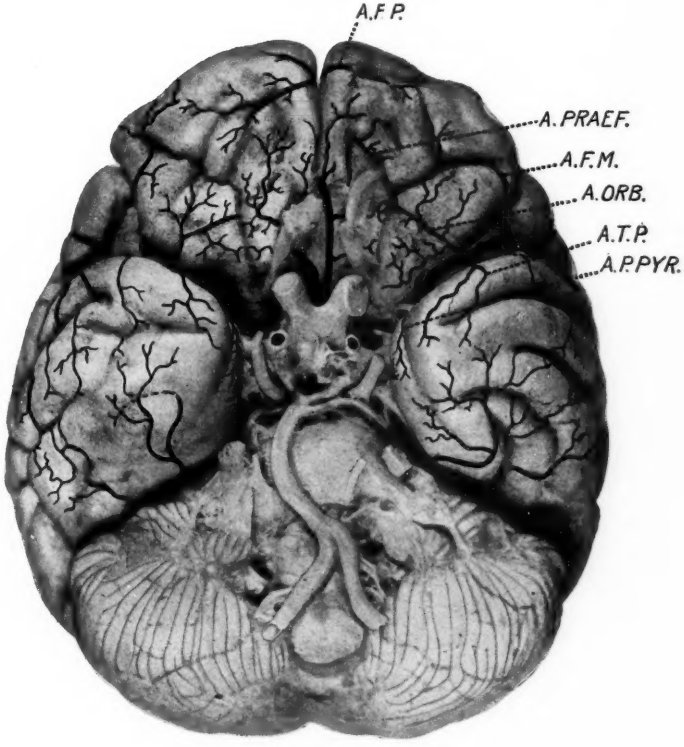

Fig. 7

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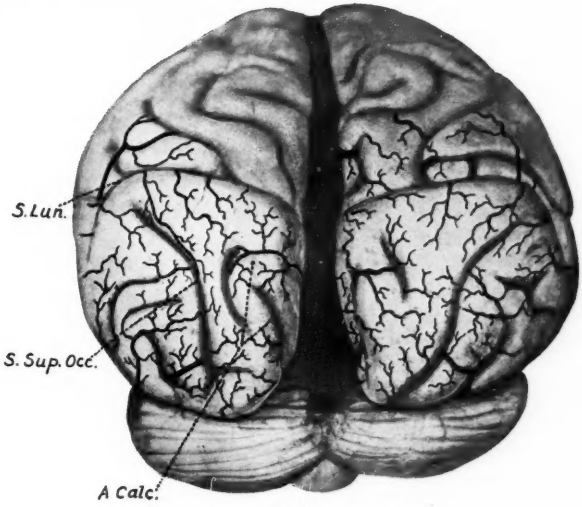

Fig. 9

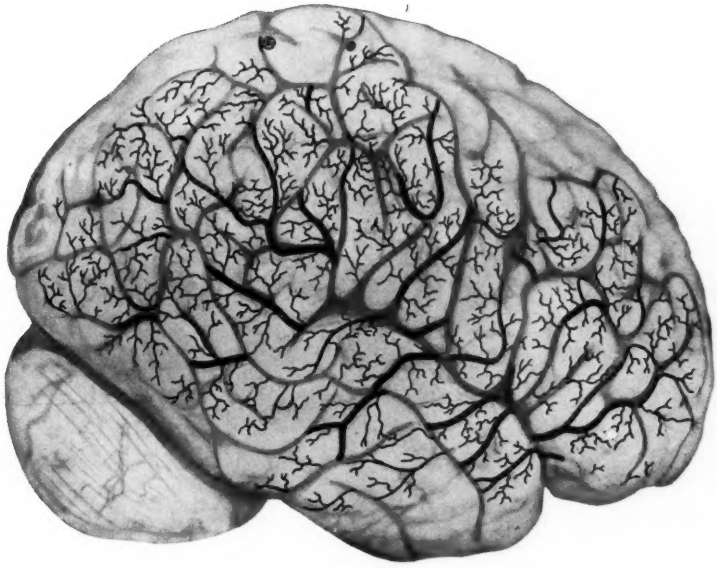

Fig. 11

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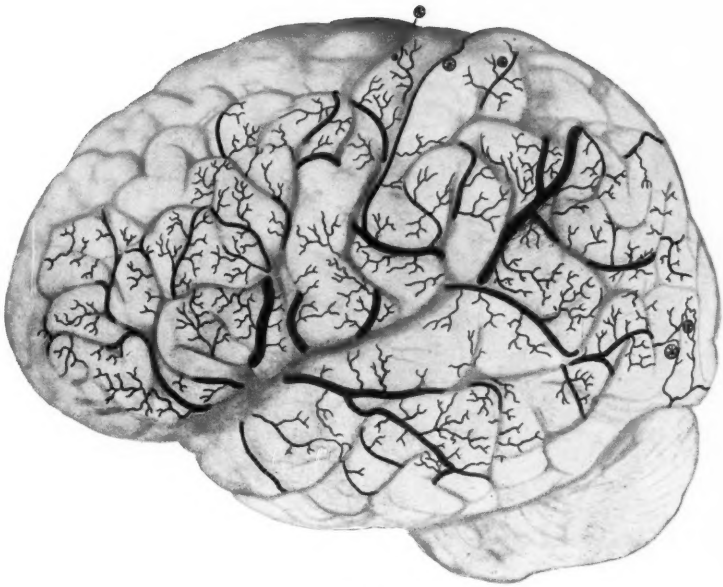

Fig. 12

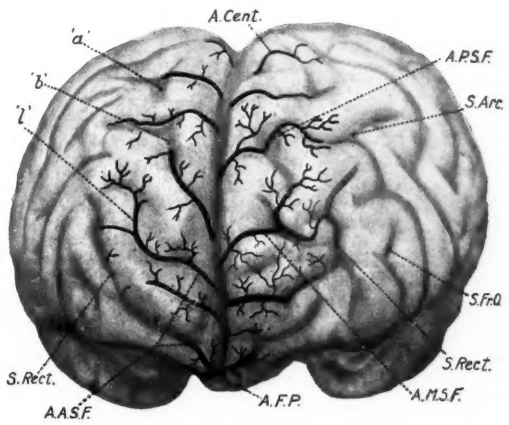

Fig. 13

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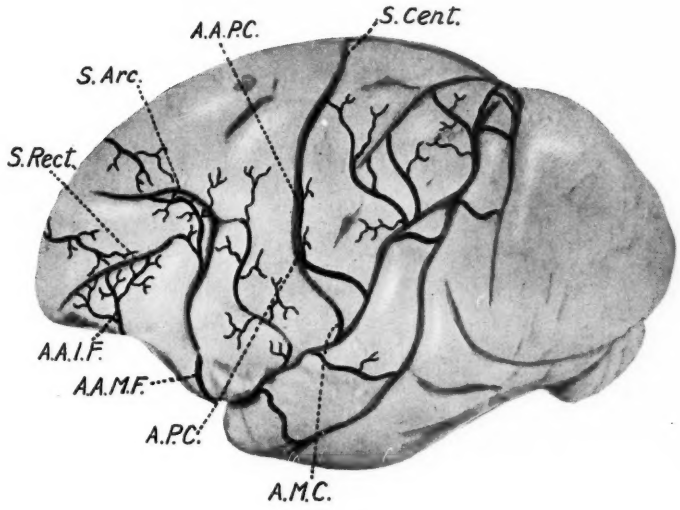
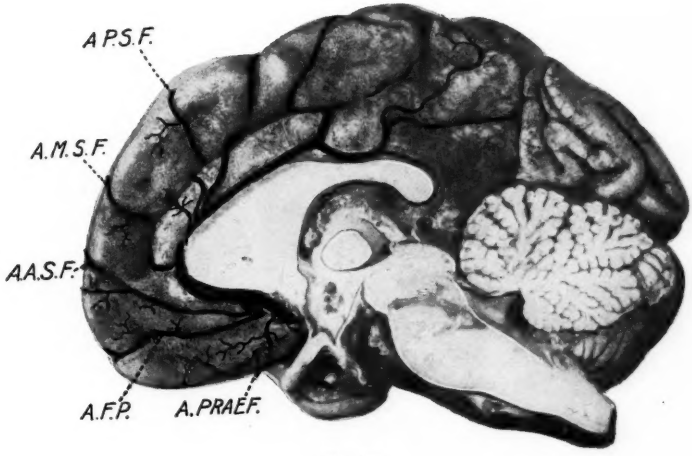


Fig. 14



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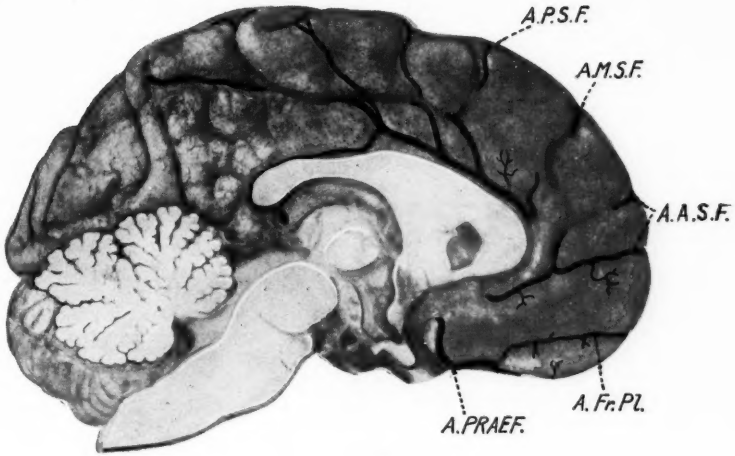

Fig. 20

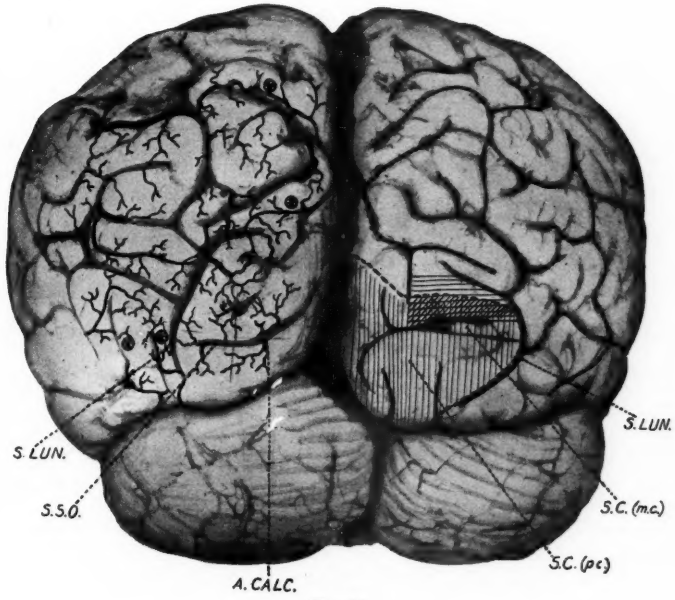

Fig. 21

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A PORTAL CIRCULATION FROM THE PITUITARY TO THE HYPOTHALAMIC REGION

By GREGOR POPA
Professor of Anatomy, University of Jassy, Roumania,
Rockefeller Foundation Fellow, University College, London,
AND UNA FIELDING
Lecturer in Neurology and Demonstrator of Anatomy,
University College, London.

THIS communication is of the nature of a preliminary note upon a peculiar and important arrangement of the vessels connecting the pituitary gland to the hypothalamus.

We have observed in the stalk (S) of the human pituitary a system of vessels arranged after the manner of a portal system, which we propose to call the hypophyseo-portal veins (1).

Although we have not been able to demonstrate the presence of any muscular tissue in the walls of these vessels, we refer to them as veins because they carry the blood away from the blood vessels distributed to the pituitary.*

Inferiorly, these vessels collect blood from the pars anterior (A), pars intermedia (I), pars tuberalis and pars posterior (P) of the pituitary. Then they ascend in the stalk (S) as parallel veins (1), which after a short course acquire thick neuroglia sheaths (14). Sometimes one glial sleeve contains several such vessels. There is no surrounding capillary net served by the vessels while they are thus ensheathed, and the tissues of the stalk between the glial cylinders appear to be without blood vessels of any sort.

Superiorly, beneath the infundibular recess of the third ventricle (III) these vessels of the portal system lose their heavy neuroglial wrapping and open out into a network of very fine channels (15). This may be called the secondary distributing net. Long processes from the ependymal cells lining the ventricle contribute to the supporting tissue of these fine vessels. This secondary net is not haphazard in its distribution in the hypothalamic region. Its connection with certain nuclear groups is at present under investigation.

The voluminous blood content of the anterior lobe of the human pituitary is brought to it by arteries (3), one on either side (in some cases more than one) springing from the internal carotid (2). As this bilateral arterial supply approaches the gland the two arteries approximate and supply the posterior lobe. Then each passes in between the glandular and nervous portions. It penetrates into the substance of the anterior lobe on its own side, carrying with it an appreciable amount of connective tissue, and then gives out its blood in all directions to the sinusoids (13).

* Since this paper was written examples of portal vessels with plain muscle in their walls have been found.

In addition to this bilateral supply from the carotids there are some fine arteries from the circle of Willis which pass along the outside of the stalk and open into the sinusoids of the pars tuberalis. There are some small venous channels corresponding to these arteries.

From the sinusoids of the pars anterior and pars intermedia some blood is returned on either side towards the place of entry of the main arterial stem, and venous channels are formed which drain out by a vein (10) following the course of the entering artery and opening into the cavernous sinus.

The whole of the blood, however, is not taken away by these bilateral venous channels (10) and the small veins of the pars tuberalis mentioned above—as has been stated already, sinusoids of the pars anterior (18), pars intermedia and pars tuberalis help in feeding the portal vessels of the stalk and so deliver blood to the secondary distribution net in the hypothalamus.

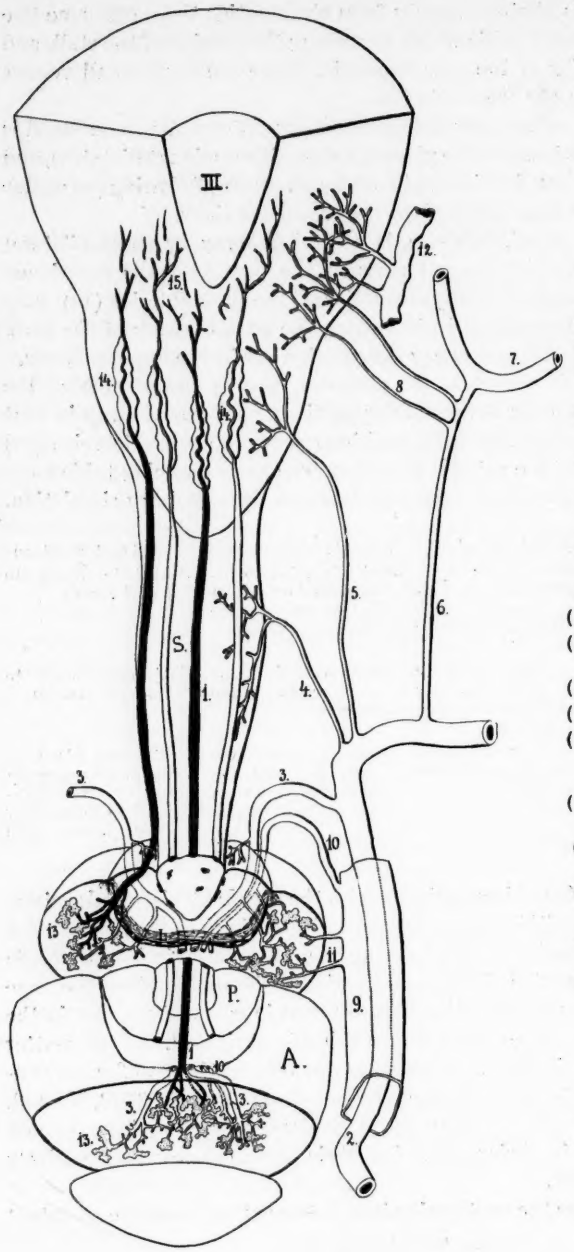
The blood which is sent into the posterior lobe by branches from the bilateral arterial supply for the glandular portion, is conveyed away in part by the hypophyseo-portal vessels (1) and in part by the systemic veins (10) following the course of the arterial branches. The accompanying table summarises the results of our observations to date upon the pituitary circulation.

Part of pituitary	Arterial supply	Systemic venous return	Portal system return
Pars anterior and pars intermedia	From carotids: a bilateral supply, usually one on each side, sometimes more than one	Systemic veins to cavernous sinus following the course of the bilateral arteries	Contribute blood to portal vessels
Pars tuberalis	From circle of Willis by small branches around the outside of the stalk	Small systemic veins corresponding to the arteries	Contributes blood to the portal vessels
Pars posterior	By branches from the bilateral supply from the carotids	By small systemic venous branches following the course of the arterial twigs	Contributes blood to the portal vessels by fine channels opening into them below their heavy glial sleeves

Colloid material is found in association with the vessels of this portal system. Sometimes it is found within the vessels (1) and sometimes in the perivascular sleeves (14). It can also be detected among the cells of certain hypothalamic nuclei. The staining reaction of the colloid varies at different levels of the same section; i.e. in the glandular portion it is different in colour from that in the hypothalamic region. These contrasts are being investigated. In the matter of colloid distribution in the hypothalamus our observations so far are confirmatory of those of Remy Collin (see *Archives de Morphologie*, 1928, No. 28). As they pass upward in the stalk the vessels of this portal system do not appear to have plain muscle in their walls,* but their lumina appear to be actively and precisely controlled.

In some hypophyses the contraction is so extreme that there are no patent

* See footnote, page 88.



(1) Hypophyseo-portal vessel
(2) Carotid artery
(3) Hypophyseal artery
(4) Small artery for pars tuberalis
(5) Small artery for tuber cinereum
(6) Posterior communicating artery
(7) Posterior cerebral artery
(8) Small arteries for infundibulum
(9) Cavernous sinus
(10) Hypophyseal vein
(11) Small hypophyseal veins
(12) Basal vein
(13) Sinusoids
(14) Heavy glial sheaths of the hypophyseo-portal veins
(15) Secondary distribution net
(A) Pars anterior of pituitary
(P) Pars posterior of pituitary
(I) Pars intermedia of pituitary
(S) Stalk

lumina. In these cases the tissue mass of the posterior lobe and stalk appears almost avascular.

Sometimes it happens that the lowest parts of these channels are widely open, where they communicate with the sinusoids, while the upper parts are constricted to a thread or absolutely closed.

In other hypophyses the hypophyseo-portal vessels are seen through their course as leashes of dilated and engorged channels which spread out superiorly into the very much finer secondary distribution net.

Work is in progress to discover how the lumina of the vessels is regulated.

Our observations indicate that the secondary distribution net is richer beneath the infundibular recess anteriorly than it is posteriorly.

A full statement of the details of our observations, with accompanying microphotographs, is being prepared.

We hope before our next publication to be able to reproduce experimentally the various conditions of the lumina of the portal vessels described above.

The observations here recorded are the result of dissection and the study of serial sections.

A NOTE ON THE MUSCLES OF THE PALATE AND THE SUPERIOR CONSTRICTOR

By J. WHILLIS, M.B., M.S.

Demonstrator of Anatomy, University of Durham

THE investigation of which the present note is the outcome was undertaken in connection with work on cleft palate and its treatment by Mr W. E. M. Wardill of Newcastle-on-Tyne. Mr Wardill called attention to the extreme

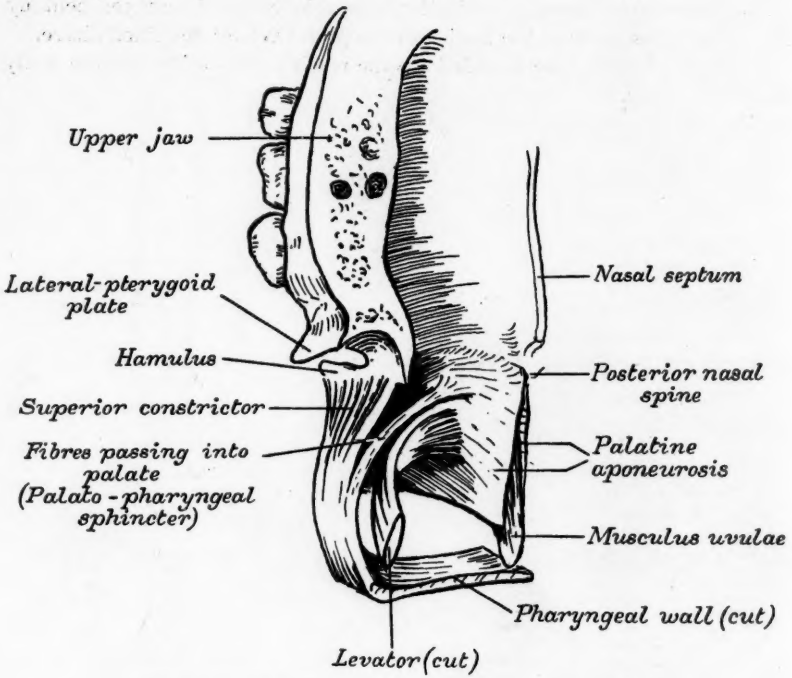


Fig. 1. The left half of the palate and pharynx from above.

importance of closure of the naso-pharyngeal isthmus in speech, and he confirmed the presence of the ridge of Passavant on the posterior pharyngeal wall at the level at which the palate abuts on it during closure. The presence of the ridge led us, in discussing the problem, to the conclusion that there must be some muscular mechanism producing it, and that the muscle fibres

must run transversely. No mention was made in Passavant's original paper of such fibres, and, to confirm their presence, I have made a series of dissections, three of which are shown in the accompanying figures. In every case similar structures have been found, so that there is probably reasonable ground for regarding what is to be described as normal.

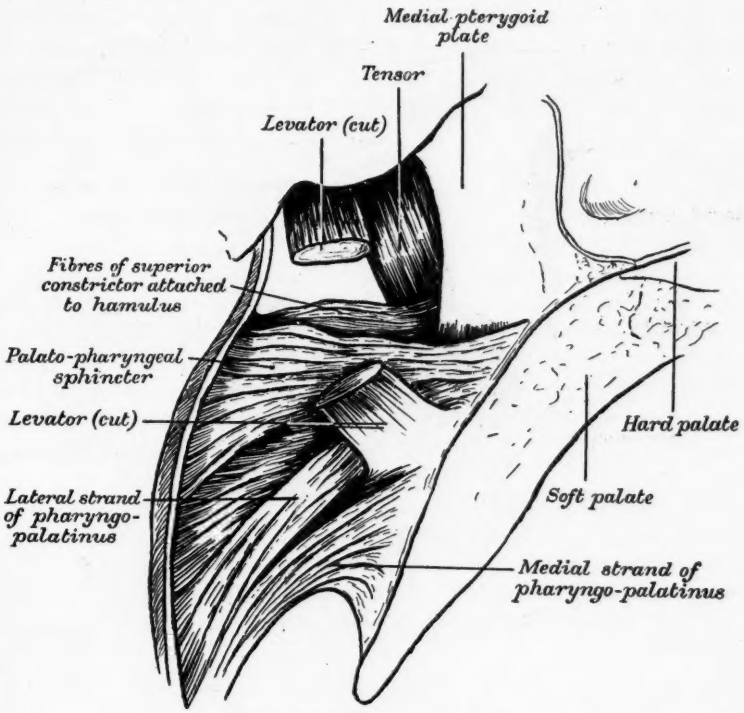


Fig. 2. The left half of the pharynx seen from the internal aspect.

Such dissections as have been made with that special purpose have confirmed Blakeway's observation that the palatal aponeurosis is formed by the expanded tendon of the tensor palati. This expansion forms an aponeurotic sheet in the anterior two-thirds of the soft palate, and to it all the other muscles of the palate are attached. The aponeurosis splits near the middle line to enclose the musculus uvulae (fig. 1).

The muscles inserted into the palatal aponeurosis are:

1. The glossopalatinus, which, springing from the side of the tongue, is attached to the inferior surface of the aponeurosis.

2. The pharyngopalatinus. This muscle arises from the pharyngeal aponeurosis and from the thyroid cartilage and, passing almost vertically

upwards on the deep surface of the constrictors, it splits into two strands. The term "strands" is more accurate than "layers" because they are in the same plane in the palate, and are separated from one another by the levator palati passing down to its insertion. The two strands finally gain attachment to the superior surface of the palatal aponeurosis, the strand medial to the levator blending with its fellow of the opposite side in the middle line (fig. 2).

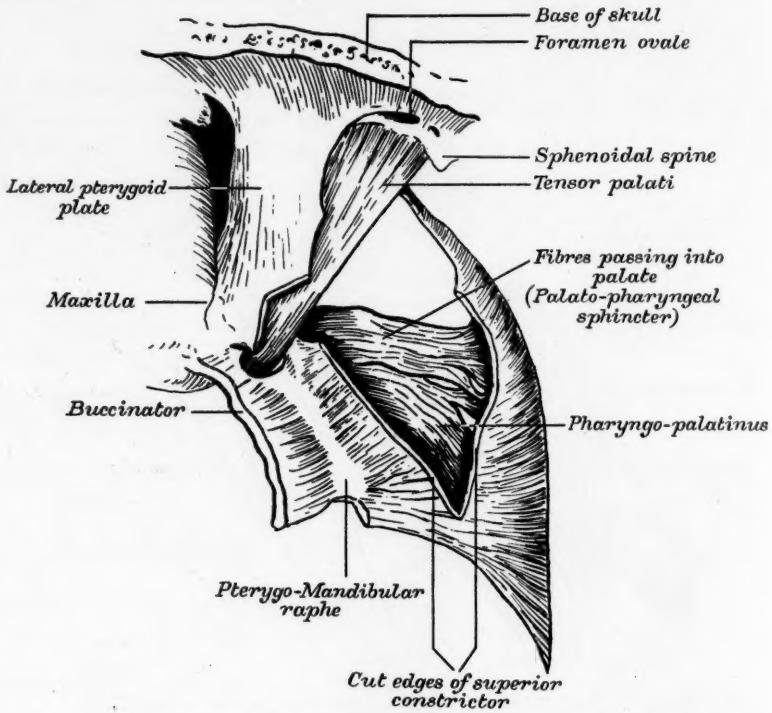


Fig. 3. The left half of the pharynx seen from the external aspect.

3. The levator palati, having entered the pharynx above the upper edge of the superior constrictor, passes obliquely downwards and medially to be inserted into the superior surface of the aponeurosis between the two strands of the pharyngopalatinus.

4. A constant band of fibres, on the same plane relative to the pharyngeal constrictors as the pharyngopalatinus, passes forwards from the superior constrictor muscle, and parallel with its upper fibres, lateral to the levator, into the palate, where it is inserted into the palatal aponeurosis (figs. 1, 2, 3). The appearance is such that the superior constrictor seems, in its upper part, to consist of two lamellae: a lateral lamella attached to the hamular process,

and a medial lamella passing into the palate. These fibres are on a level with the ridge of Passavant as observed in the living. In every case it has been found that quite a large branch of the ascending pharyngeal artery passes downwards between this muscle band and the upper fibres of the superior constrictor. It is interesting to note also that the change in character of the mucosa on the upper surface of the palate from the nasal columnar type to the pharyngeal squamous type takes place where the muscle is inserted. The most suitable name for this muscle, if it merit a place in terminology, is that of "palato-pharyngeal sphincter," as its action appears to be that it assists in shutting off the naso-pharynx by producing the ridge of Passavant on the posterior pharyngeal wall.

One other point has been brought out by these dissections, and that is that in none of the specimens have any actual muscle fibres of the superior constrictor been found attached to the lower half of the medial pterygoid plate. Above the hamulus the bucco-pharyngeal fascia and pharyngeal aponeurosis are attached to the posterior border of the lamina, but no actual muscle is to be seen, the attachment of the latter being limited to the hamulus.

I wish to express my thanks to Mr W. E. M. Wardill and Prof. R. B. Green for the help and encouragement they have given me, and to Prof. J. E. Frazer who, in a personal communication, has kindly given me information which tends to confirm the observations from a developmental standpoint.

SUMMARY

It would appear that there is a constant band of muscle fibres passing from the superior constrictor into the palate, and that these fibres are on a level with the ridge of Passavant. It is suggested that they play an important part in shutting off the naso-pharynx, and that the name of palato-pharyngeal sphincter should be given to them.

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THE ENDOCRANIAL EQUIVALENTS OF THE FRANKFURT PLANE AND THE EXOCRANIAL POSITION OF THE INTERNAL AUDITORY MEATUS

By LT.-COL. L. A. HODGKINSON LACK, I.M.S.
Professor of Anatomy, University of Rangoon

During the period June 1924 to March 1928 while engaged in the routine work of helping medical students to prepare themselves for the Second Professional Examination in Anatomy there was not much leisure to devote to any detailed study of the crania of the various indigenous races of Burma. At that time I was aware only of the paper published by the late Sir William Turner in vol. xxxix, Pt iii, of the *Transactions of the Royal Society of Edinburgh*; this paper dealt with 44 crania obtained from Burma and it contained no specimens of the crania of Chingpaws (usually referred to wrongly as "Kachins"), and there were but one Karen and but two Shan representatives.

Therefore it appeared advisable that a part of the work of the Department of Anatomy in the University of Rangoon should be the compilation of measurements of the crania of the different indigenous races of Burma in order to supplement the knowledge of them already available in the paper mentioned above, but unfortunately I had no means at my disposal of doing accurate work.

On going to Edinburgh in April 1928 and on placing the facts before Prof. Arthur Robinson he most kindly gave me access to the crania mentioned above and enabled me to get a set of craniograms of these crania. A preliminary study of these craniograms has been made and it is hoped that in due time the results will be published.

While engaged in the course of this study it appeared advisable to ascertain the endocranial equivalents of the Frankfurt plane with reference to some easily recognisable points on the surface of the brain, so that it would be possible to project the Frankfurt plane on to the surface of the brain, that is to say, to orient an endocranial cast on the Frankfurt plane.

It so happened that the first skull traced (XXVI E. 10) showed the Frankfurt plane passing 5 mm. above the centre of the lower border of the internal auditory meatus and through the point on the superior border of the lateral sinus where it began to change its direction, that is to say, points which could be found easily on an endocranial cast and on a well hardened brain.

At the same time it appeared advisable to ascertain the position of the internal auditory meatus relative to the highest point of the external auditory meatus and to the posterior root of the zygoma, immediately above the point mentioned, as a fact of some surgical utility.

Fortunately there were available in the Anatomical Museum of the University of Edinburgh 107 crania which had been sectioned parallel to the sagittal plane and these provided the material for the study detailed below.

Each skull was placed in the craniograph with the sagittal plane vertical and with the Frankfurt plane horizontal, and the measurements were made in that position and recorded immediately.

Some little time after the study detailed below had been completed, my attention was invited by Prof. Robinson to "A study of the Hokien and the Tamil Skull," by Prof. Gordon Harrower, of the King Edward VII Medical College, Singapore, published in vol. LIV, Pt III (No. 13) of the *Transactions of the Royal Society of Edinburgh*. This led me to M. L. Tildesley's "First Study of the Burmese Skull," published in vol. XIII, Nos. 2 and 3 of *Biometrika* for July 1921. There came to hand later on "A Study of the Crania of the Hylam Chinese, etc.," by Prof. Harrower, published in vol. XX B, Pts 3 and 4 of *Biometrika* for December 1928.

While these papers have no direct bearing on the points dealt with in the study detailed below they are concerned very closely with the work being done on the crania studied by Sir William Turner, to which reference has been made above.

It is hoped that as time passes and as material becomes available a sufficient series of records will be obtained to supplement the work published in the above papers, particularly Tildesley's, by giving information about the cranial measurements of Shans, Chingpaws and Karens.

RACIAL DIFFERENTIATION

The 107 crania mentioned above may be divided more or less accurately on the following lines with the results summarised in the table printed hereunder:

	Relation to the centre of the lower border of the internal auditory meatus			Relation to the point at which the superior border of the lateral sinus begins to change its direction		
	+	−	0·0*	+	−	0·0*
I.	5 = 11·0	5 = 13·0	5 = 0·0	1 = 4·0	13 = 146·0	1 = 0·0
I. A.	—	2 = 7·5	—	—	—	2 = 0·0
I. B.	2 = 4·25	—	—	—	1 = 12·0	1 = 0·0
II.	3 = 9·4	7 = 20·5	1 = 0·0	2 = 9·0	6 = 43·0	3 = 0·0
III.	1 = 1·5	7 = 17·0	2 = 0·0	2 = 85·0	8 = 62·5	—
III. A.	—	1 = 3·0	—	—	1 = 13·0	—
III. B.	1 = 4·0	1 = 2·0	—	—	2 = 17·0	—
IV.	1 = 22·5	8 = 17·0	—	—	9 = 126·0	—
V.	9 = 16·5	5 = 14·0	5 = 0·0	—	19 = 210·5	—
VI.	15 = 43·5	7 = 18·0	1 = 0·0	7 = 27·0	14 = 95·5	2 = 0·0
VII.	1 = 1·0	8 = 24·5	—	—	9 = 95·5	—
VIII.	2 = 13·0	2 = 2·5	—	—	3 = 68·0	1 = 0·0
	40 = 106·65	53 = 139·0	14 = 0·0	12 = 48·5	85 = 889·0	10 = 0·0
	∴ 1 = 2·66	∴ 1 = 2·62		∴ 1 = 4·04	∴ 1 = 10·4	
		+ = 2·66			− = 10·4	
		− = 2·62			+ = 4·04	
		Diff. = +0·04			Diff. = −6·36	
Eliminating the microcephalics:						
	38 = 93·65	51 = 136·5	14 = 0·0	12 = 48·5	82 = 821·0	9 = 0·0
	∴ 1 = 2·46	∴ 1 = 2·67		∴ 1 = 4·04	∴ 1 = 10·01	
		− = 2·67			− = 10·01	
		+ = 2·46			+ = 4·04	
		Diff. = −0·21			Diff. = 5·97	

* + = above; − = below; 0·0 = at the point.

That is to say, the Frankfurt plane lies 0·21 mm. below the centre of the lower border of the internal auditory meatus and 5·97 mm. below the point at which the superior border of the lateral sinus begins to change its direction.

In the different races the position of the Frankfurt plane is as follows:

		Relation to the centre of the lower border of the internal auditory meatus (mm.)	Relation to the point at which the superior border of the lateral sinus begins to change its direction (mm.)
I.	African and allied crania	0·4 below	7·2 below
I. A.	North African crania	3·75 „	At the point
I. B.	Arctic crania	2·12 above	6·0 below
II.	British crania	0·43 below	2·66 „
III.	Indian crania	0·92 „	3·55 „
III. A.	Andaman Islander	3·0 „	13·0 „
III. B.	Malaysian crania	2·0 above	8·5 „
IV.	Mongolian crania:		
	(*a*) Chins	0·5 „	10·0 „
	(*b*) Siamese	2·3 below	19·0 „
	(*c*) Chinese	2·0 „	10·0 „
	(*d*) Burmese	2·0 „	19·0 „
V.	Polynesian crania	0·97 „	11·08 „
VI.	Australian crania	0·33 above	2·95 „
VII.	Amerindian crania:		
	(*a*) North Amerindians ...	3·75 below	9·25 „
	(*b*) South Amerindians ...	1·83 „	11·0 „
VIII.	Microcephalics	5·25 above	17·0 „

The individual measurements are shown in the tables printed hereunder:

Frankfurt plane endocranial equivalents

Serial no.	Catalogue no.	Sex and age	Relation to the centre of the lower border of the internal auditory meatus (mm.)	Relation to the point at which the superior border of the lateral sinus begins to change its direction (mm.)	Race, etc.
			I. African and Allied crania (15)		
1	XXVI. E. 10	—	+5·0	0	Kaffir
37	XXVI. A. 16	—	0	− 7·0	Assouan; Upper Egypt
40	XXVI. B. 1	—	+1·0	− 4·0	Nyassaland
41	XXVI. D. 3	—	−3·0	−13·0	West African; Old Calabar
42	XXVI. D. 9	—	−3·0	−26·0	„ „
43	XXVI. E. 1	M. 25	−3·0	−12·0	S.W. African; Damara
44	XXVI. E. 2	—	0	−11·0	Kaffir
45	XXVI. E. 3	—	+1·0	−11·0	„
46	XXVI. E. 4	F. 45	0	−10·0	„
47	XXVI. E. 18	—	−1·5	− 6·0	Bushman; S. Africa
48	XXVI. E. 21	M.	+3·0	+ 4·0	„ „
49	XXVI. E. 34	—	0	−16·0	Zulu; S. Africa
50	XXVI. F. 5	M.	+1·0	− 1·0	Negro
51	XXVI. F. 20	M. 28	−2·5	−13·0	„
52	XXVII. 4	—	0	−16·0	Madagascar
			I. A. North African crania (2)		
38	XXVI. A. 62	—	−2·5	0	Guanche; Teneriffe
39	XXVI. A. 63	—	−5·0	0	„ „

Serial no.	Catalogue no.	Sex and age	Relation to the centre of the lower border of the internal auditory meatus (mm.)	Relation to the point at which the superior border of the lateral sinus begins to change its direction (mm.)	Race, etc.
			I. B. Arctic crania (2)		
13	XVI. C. 6	—	+1·75	−12·0	Esquimau
14	XVI. C. 15	—	+2·5	0	,,
			II. British crania (11)		
2	I. A. 12	M. adult	+4·5	0	English
3	I. A. 13	M. adult	−1·1	− 6·0	,,
4	I. A. 16	M. adult	−1·4	+ 5·0	,,
5	I. B. 58	M. adult	−3·0	0	Scots; Ratho
6	I. B. 28	M. adult	+2·4	− 1·0	Scots; Kirk o' Field
7	I. B. 55	—	−4·0	− 8·0	Scots; Ratho
8	I. B. 212 A	—	+2·5	0	Scots; Lundin Links
9	I. B. 213	—	0	−10·0	Scots; Culross Abbey
10	I. B. 216	—	−4·0	+ 4·0	Scots; Oban
11	I. B. 230	—	−6·0	−15·0	Scots; Nether Urquhart
12	I. B. 238	—	−1·0	− 3·0	Scots; Coldingham
			III. Indian crania (10)		
15	XXI. A. 22	M.	−1·0	− 5·0	Ooryia; Orissa
16	XXI. A. 28	F. 24	0	− 9·0	Bengal
17	XXI. A. 31	—	−7·0	−13·0	Hindu
18	XXI. B. 4	M.	−1·0	− 5·0	Gond; Godavery
19	XXI. B. 9	M.	+1·5	−12·5	Bhil; Alirajpore
20	XXI. B. 10	F.	−2·0	− 8·0	,, ,,
21	XXI. D. 10	—	0	+ 7·0	Tamil; Sudra
24	XXI. G. 3	—	−2·0	+ 1·5	Ceylonese; Malabar Coast
25	XXI. H. 4	M.	−2·0	− 6·0	Ceylonese; Veddah
26	XXI. H. 6	M.	−2·0	− 4·0	,, ,,
			III. A. Andaman Islanders (1)		
32	XXII. D. 6	F.	−3·0	−13·0	Andamans
			III. B. Malaysian crania (2)		
33	XXII. F. 1	—	+4·0	− 6·0	N. Borneo
31	XXII. C. 15	F.	−2·0	−11·0	Malay
			IV. Mongolian crania (9)		
22	XXI. F. 7	M.	−2·0	−18·0	Manipur; Chin Lushai
23	XXI. F. 10	M.	+2·5	− 2·0	Chin; Tiddim
27	XXII. A. 1	F.	−1·0	−15·0	Siamese
28	XXII. A. 4	Juvenile	−3·0	−20·0	,,
29	XXII. A. 5	F.	−3·0	−22·0	,,
30	XXI. K. 10	M. aged	−2·0	−19·0	,,
34	XXIV. B. 5	M.	−2·0	− 5·0	Chinese
35	XXIV. B. 6	M.	−3·0	− 8·0	,,
36	XXIV. B. 15	—	−1·0	−17·0	,,
			V. Polynesian crania (19)		
53	XXVIII. A. 18	—	+2·0	− 7·0	New Guinea; Torres Straits
54	XXVIII. A. 24	? F. aged	+4·0	− 7·0	New Guinea; Port Wesley
55	XXVIII. A. 29	—	+0·5	− 9·0	New Guinea
56	XXVIII. A. 30	—	0	−17·5	,,
57	XXVIII. A. 32	—	+2·0	− 6·0	,,
58	XXVIII. A. 34	—	+1·0	− 7·0	,,
59	XXVIII. A. 35	—	+1·0	− 3·0	,,
60	XXVIII. B. 2	—	−2·0	− 4·0	Loyalty Island

Serial no.	Catalogue no.	Sex and age	Relation to the centre of the lower border of the internal auditory meatus (mm.)	Relation to the point at which the superior border of the lateral sinus begins to change its direction (mm.)	Race, etc.
			V. Polynesian crania (19) (*cont.*)		
61	XXVIII. C. 28	—	0	−11·5	New Hebrides
62	XXVIII. C. 32	F.	0	− 7·5	,,
63	XXVIII. C. 33	—	+3·0	− 6·0	,,
64	XXVIII. F. 45	24	−1·5	−22·0	Sandwich Islands
65	XXVIII. G. 1	—	−2·0	−22·0	Chatham Islands; Maori
66	XXVIII. G. 5	—	−4·5	− 9·0	,, ,,
67	XXVIII. G. 17	—	−4·0	−15·0	,, ,,
68	XXVIII. H. 4	M.	+1·5	−19·5	New Caledonia; Kanaka
69	XXVIII. H. 12	—	0	−10·5	,, ,,
70	XXVIII. H. 17	—	0	− 6·0	,, ,,
83	XXXI. A. 27	—	+1·5	−21·0	Auckland; New Zealand*
			* Probably Maori.		
			VI. Australian crania (23)		
71	XXIX. A. 10	F.	+2·0	+ 7·0	Queensland
72	XXIX. A. 11	—	+0·5	− 3·0	,,
73	XXIX. A. 14	—	−2·5	+ 5·0	,,
74	XXIX. B. 3	—	−0·5	−17·5	New South Wales
75	XXIX. B. 5	—	−3·0	− 3·5	,, ,,
76	XXIX. B. 12	M.	+2·5	0	,, ,,
77	XXIX. C. 10	M. adult	+3·5	+ 2·0	Victoria
78	XXIX. C. 18	—	−3·0	0	,,
79	XXIX. D. 3	—	+1·0	+ 1·0	Northern Territory
80	XXIX. G. 17	F.	0	−10·5	Central Australia
81	XXX. 2	M. adult	−4·0	− 7·0	Tasmania
82	XXX. 5	M. adult	−2·5	− 9·5	Van Dieman's Land
96	XXIX. D. 17	—	+6·0	+ 2·5	Northern Territory
97	XXIX. D. 18	—	+1·5	−14·0	,, ,,
98	XXIX. D. 20	—	−2·5	− 4·0	,, ,,
99	XXIX. D. 29	—	+5·0	+ 2·0	,, ,,
100	XXIX. D. 43	—	+2·5	− 3·0	,, ,,
101	XXIX. D. 45	—	+3·0	− 1·0	,, ,,
102	XXIX. D. 61	—	+0·5	−10·5	,, ,,
103	XXIX. D. 66	—	+4·5	− 2·5	,, ,,
104	XXIX. D. 73	—	+4·0	− 6·0	,, ,,
105	XXX. 1	M. adult	+5·0	− 3·5	Tasmania
107	XXIX. D. 28	—	+2·0	+ 7·5	Northern Territory
			VII. Amerindian crania (9)		
84	XXXII. A. 1	—	−4·0	−12·0	Chinook; N. America
85	XXXII. A. 3	—	−3·5	− 6·5	,, ,,
86	XXXIII. A. 3	—	+1·0	−11·0	Peruvian
87	XXXIII. A. 6	—	−1·5	−16·0	,,
88	XXXIII. A. 26	—	−2·0	−14·0	,,
89	XXXIII. A. 33	—	−1·5	−16·0	Peruvian; Inca Cemetery
90	XXXIII. B. 4	M.	−5·0	− 6·5	Chile
91	XXXIII. C. 6	—	−5·0	− 7·5	Patagonia
106	XXXIII. C. 4	M.	−2·0	− 6·0	Tierra del Fuego
			VIII. Microcephalic crania (4)		
92	XXXV. A. 1	M.	−1·5	− 8·0	Scots
93	XXXV. A. 2	F. young	−1·0	0	,,
94	XXXV. A. 6	M. 60	+7·0	−30·0	Scots? Irish?
95	XXXV. A. 7	M. 19	+6·0	−30·0	Scots

CRANIAL INDEX DIFFERENTIATION

A reference to the table in the second part of this paper shows that these 107 crania can be classified as 86 Dolichocephalic, 17 Brachycephalic and 4 Microcephalic, of which three are Dolichocephalic and one approximately Brachycephalic.

The summary of their relationships is shown in the table printed hereunder:

Relation to the centre of the lower border of the internal auditory meatus			Relation to the point at which the superior border of the lateral sinus begins to change its direction		
Dolichocephalics			**Dolichocephalics**		
+	−	0·0	+	−	0·0
36 = 89·65	36 = 97·5	14 = 0·0	11 = 44·5	67 = 608·5	8 = 0·0
∴ 1 = 2·49	∴ 1 = 2·70		∴ 1 = 4·04	∴ 1 = 9·08	
	− = 2·70			− = 9·08	
	+ = 2·49			+ = 4·04	
	Diff. = −0·21			Diff. = −5·01	
Brachycephalics			**Brachycephalics**		
+	−	0·0	+	−	0·0
2 = 4·00	15 = 39·0	0 = 0·0	1 = 4·0	15 = 212·0	1 = 0·0
∴ 1 = 2·0	∴ 1 = 2·6		∴ 1 = 4·0	∴ 1 = 14·1	
	− = 2·6			− = 14·1	
	+ = 2·0			+ = 4·0	
	Diff. = − 0·6			Diff. = −10·1	
Microcephalics			**Microcephalics**		
+	−	0·0	+	−	0·0
2 = 13·0	2 = 2·5	0 = 0·0	—	3 = 68·0	1 = 0·0
∴ 1 = 6·5	∴ 1 = 1·25		∴ 4 = 68·0	∴ 1 = 17	
	+ = 6·5			+ = 0·0	
	− = 1·25			− = 17·0	
	Diff. = + 5·25			Diff. = −17·0	

+ = above; − = below; 0·0 = at the point.

That is to say:

(*a*) In Dolichocephalic crania the Frankfurt plane lies 0·21 mm. below the centre of the lower border of the internal auditory meatus, and 5·01 mm. below the point at which the superior border of the lateral sinus begins to change its direction.

(*b*) In Brachycephalic crania the Frankfurt plane lies 0·6 mm. below the centre of the lower border of the internal auditory meatus, and 10·1 mm. below the point at which the superior border of the lateral sinus begins to change its direction.

(*c*) In Microcephalic crania the Frankfurt plane lies 5·25 mm. above the centre of the lower border of the internal auditory meatus, and 17 mm. below the point at which the superior border of the lateral sinus begins to change its direction.

Summing up the series, but eliminating the microcephalics, the relations are as shown in the table printed hereunder:

Relation to the centre of the lower border of the internal auditory meatus			Relation to the point at which the superior border of the lateral sinus begins to change its direction		
+	−	0·0	+	−	0·0
36 = 89·65	36 = 97·5	14 = 0·0	11 = 44·5	67 = 608·5	8 = 0·0
2 = 4·00	15 = 39·0	0 = 0·0	1 = 4·0	15 = 212·0	1 = 0·0
∴ 38 = 93·65	∴ 51 = 136·5	∴ 14 = 0·0	∴ 12 = 48·5	∴ 82 = 820·5	∴ 9 = 0·0
∴ 1 = 2·46	∴ 1 = 2·67		∴ 1 = 4·04	∴ 1 = 10·0	
	− = 2·67			− = 10·0	
	+ = 2·46			+ = 4·04	
	Diff. = −0·21			Diff. = −5·96	

\+ = above; − = below; 0·0 = at the point.

That is to say, the Frankfurt plane lies 0·21 mm. below the centre of the lower border of the internal auditory meatus and 5·96 mm. below the point at which the superior border of the lateral sinus begins to change its direction.

Therefore more or less the Frankfurt plane may be indicated on the surface of an endocranial cast or of a well hardened brain by a line drawn from the superficial origin of the VIIth and VIIIth cranial nerves to the *centre* of the lateral sinus where it begins to change its direction.

THE EXOCRANIAL POSITION OF THE INTERNAL AUDITORY MEATUS: RACIAL DIFFERENTIATION

Again dividing these 107 crania on racial lines the results are summarised in the table printed hereunder:

	Horizontal to the highest point of the external auditory meatus			Vertical to the highest point of the external auditory meatus			Mesial to zygoma
	+	−	0·0	+	−	0·0	
I.	—	12 = 69·4	3 = 0·0	7 = 17·0	7 = 14·5	1 = 0·0	15 = 543·1
I. A.	2 = 9·8	—	—	2 = 4·5	—	—	2 = 74·2
I. B.	—	2 = 9·9	—	—	2 = 2·5	—	2 = 78·3
II.	1 = 2·6	7 = 52·9	3 = 0·0	5 = 18·5	4 = 9·0	2 = 0·0	11 = 395·4
III.	2 = 9·9	7 = 58·5	1 = 0·0	7 = 15·5	3 = 5·5	—	10 = 341·2
III. A.	—	1 = 2·8	—	1 = 3·0	—	—	1 = 35·8
III. B.	—	2 = 7·5	—	1 = 1·0	1 = 2·5	—	2 = 72·3
IV.	3 = 11·4	6 = 51·8	—	6 = 15·5	—	3 = 0·0	9 = 336·3
V.	5 = 17·9	10 = 40·5	4 = 0·0	9 = 21·0	9 = 12·0	1 = 0·0	19 = 702·0
VI.	1 = 4·0	19 = 120·7	3 = 0·0	9 = 22·0	14 = 38·5	—	23 = 836·0
VII.	2 = 88·4	7 = 34·4	—	8 = 30·0	—	1 = 0·0	9 = 361·2
VIII.	—	4 = 36·9	—	1 = 2·5	3 = 11·5	—	4 = 119·7
	16 = 64·0	77 = 485·3	14 = 0·0	56 = 150·5	43 = 96·0	8 = 0·0	107 = 3895·5
Eliminating the microcephalics:							
	16 = 64·0	73 = 448·4		55 = 148·0	40 = 84·5		103 = 3775·8
	∴ 1 = 4·0	∴ 1 = 6·14		∴ 1 = 2·69	∴ 1 = 2·11		∴ 1 = 36·6
		− = 6·14			+ = 2·69		
		+ = 4·00			− = 2·11		
		Diff. = −2·14			Diff. = +0·58		

\+ = above or anterior; − = below or posterior; 0·0 = at the point.

That is to say, the centre of the lower border of the internal auditory meatus lies 2·14 mm. posterior and 0·58 mm. superior to the highest point of the external auditory meatus and 36·6 mm. mesial to the posterior root of the zygoma immediately above the highest point of the external auditory meatus.

In the different races the position of the centre of the lower border of the internal auditory meatus is as follows:

Race	Relation to the highest point of the external auditory meatus		Mesial to the posterior root of the zygoma (mm.)
	Horizontal (mm.)	Vertical (mm.)	
I. African and Allied crania ...	4·6 post.	0·35 sup.	36·9
I. A. North African crania ...	4·9 ant.	2·25 „	37·1
I. B. Arctic crania	4·95 post.	1·25 inf.	39·15
II. British crania	4·95 „	1·45 sup.	35·9
III. Indian crania	3·4 „	0·38 „	34·1
III. A. Andaman Islander	2·8 „	3·0 „	35·8
III. B. Malaysian crania	3·75 „	1·5 inf.	36·15
IV. Mongolian crania:			
(*a*) Chins	4·6 ant.	1·75 sup.	39·3
(*b*) Siamese	9·7 post.	2·16 „	34·1
(*c*) Chinese	6·85 „	0·5 „	38·5
(*d*) Burmese	4·6 „	4·0 „	39·6
V. Polynesian crania	0·47 „	1·0 „	37·0
VI. Australian crania	2·35 „	0·35 inf.	36·3
VII. Amerindian crania:			
(*a*) North Amerindians ...	6·4 „	3·0 sup.	41·6
(*b*) South Amerindians ...	0·12 „	3·4 „	39·7
VIII. Microcephalic crania ...	9·25 „	1·33 inf.	29·9

The individual measurements are shown in the tables hereunder:

The position of the centre of the lower border of the internal auditory meatus relative to the highest point of the external auditory meatus and to the posterior root of the zygoma

Serial no.	Catalogue no.	Length	Width	Cranial index	Class	Relation of centre of lower border of internal auditory meatus: Horizontal to external auditory meatus (mm.)	Vertical to external auditory meatus (mm.)	Mesial to posterior root of zygoma (mm.)
			I. African and Allied crania (15)					
1	XXVI. E. 10	1884	1330	70·5	D	− 6·0	−3·5	41·0
37	XXVI. A. 16	1925	1326	68·8	D	− 7·5	−2·0	36·6
40	XXVI. B. 1	1825	1315	71·0	D	− 7·3	−2·0	36·0
41	XXVI. D. 3	1582	1182	75·9	M (D)	0	+1·5	37·6
42	XXVI. D. 9	1828	1285	70·2	D	−16·2	+3·0	33·7
43	XXVI. E. 1	1787	1322	73·9	D	− 7·1	+4·0	36·5
44	XXVI. E. 2	1791	1385	77·3	M (D)	− 1·3	+1·0	38·2
45	XXVI. E. 3	1866	1350	72·3	D	− 2·0	−1·0	38·4
46	XXVI. E. 4	1787	1278	71·5	D	− 2·0	0	36·0
47	XXVI. E. 18	1679	1159	69·0	D	− 5·0	+1·0	31·9
48	XXVI. E. 21	1675	1328	79·2	M (B)	−11·0	−3·5	31·2
49	XXVI. E. 34	1816	1307	71·9	D	0	−1·5	36·0
50	XXVI. F. 5	1884	1422	75·4	M (D)	0	−1·0	36·4
51	XXVI. F. 20	1891	1358	71·8	D	− 1·6	+3·5	36·4
52	XXVII. 4	1886	1336	70·8	D	− 2·3	+3·0	35·2

Serial no.	Catalogue no.	Length	Width	Cranial index	Class	Relation of centre of lower border of internal auditory meatus: Horizontal to external auditory meatus (mm.)	Vertical to external auditory meatus (mm.)	Mesial to posterior root of zygoma (mm.)
			I. A. North African crania (2)					
38	XXVI. A. 62	1777	1300	73·1	D	+ 6·3	+2·0	35·9
39	XXVI. A. 63	1697	1353	79·7	M (B)	+ 3·5	+2·5	38·3
			I. B. Arctic crania (2)					
13	XVI. C. 6	1803	1255	69·6	D	− 2·9	−1·0	39·8
14	XVI. C. 15	1816	1340	73·7	D	− 7·0	−1·5	38·5
			II. British crania (11)					
2	I. A. 12	1751	1236	70·5	D	− 5·3	−3·0	35·0
3	I. A. 13	1940	1368	70·5	D	0	−2·0	35·0
4	I. A. 16	1833	1400	76·3	M (D)	0	+1·0	36·0
5	I. B. 58	1867	1369	73·3	D	− 5·5	+3·5	37·0
6	I. B. 28	1867	1362	72·9	D	0	0	36·3
7	I. B. 55	1833	1431	78·0	M (D)	+ 2·6	+3·5	34·5
8	I. B. 212 A	1844	1315	71·5	D	−10·4	−3·5	35·1
9	I. B. 213	1790	1334	74·5	D	−13·7	−0·5	35·0
10	I. B. 216	2033	1390	68·3	D	− 6·8	+4·0	37·7
11	I. B. 230	1826	1344	73·0	D	− 8·2	+6·5	34·8
12	I. B. 238	1852	1416	76·4	B (D)	− 3·0	0	39·0
			III. Indian crania (10)					
15	XXI. A. 22	1839	1322	71·8	D	− 5·7	+2·0	33·7
16	XXI. A. 28	1658	1188	71·6	D	−11·2	−2·0	34·6
17	XXI. A. 31	1830	1368	74·7	D	+ 3·6	+7·5	36·2
18	XXI. B. 4	1762	1167	66·1	D	− 8·8	−1·5	33·0
19	XXI. B. 9	1723	1242	72·0	D	− 9·5	−2·0	34·4
20	XXI. B. 10	1724	1188	68·9	D	0	+1·0	31·4
21	XXI. D. 10	1737	1259	72·4	D	−11·6	+1·0	31·0
24	XXI. G. 3	1822	1362	74·2	D	− 8·0	+1·5	34·2
25	XXI. H. 4	1697	1275	75·1	M (D)	− 3·7	+1·5	36·3
26	XXI. H. 6	1753	1292	73·7	D	+ 6·3	+1·0	36·4
			III. A. Andaman Islanders (1)					
32	XXII. D. 6	1603	1276	79·6	M (B)	− 2·8	+3·0	35·8
			III. B. Malaysian crania (2)					
33	XXII. F. 1	1772	1311	73·9	D	− 1·0	−2·5	36·5
31	XXII. G. 15	1670	1305	78·1	M (B)	− 6·5	+1·0	35·8
			IV. Mongolian crania (9)					
22	XXI. F. 7	1825	1302	71·3	D	+ 5·7	+2·5	40·0
23	XXI. F. 10	1677	1292	77·0	M (D)	+ 3·5	+1·0	38·6
27	XXII. A. 1	1662	1306	78·5	M (B)	− 8·7	0	34·5
28	XXII. A. 4	1650	1333	80·7	B	−15·4	+4·0	32·7
29	XXII. A. 5	1691	1306	77·2	M (B)	− 5·4	+2·5	35·2
30	XXI. K. 10	1663	1522	91·5	B	− 4·6	+4·0	39·6
34	XXIV. B. 5	1674	1379	82·3	B	− 9·3	0	36·3
35	XXIV. B. 6	1768	1295	73·2	D	− 8·8	+1·5	38·6
36	XXIV. B. 15	1594	1380	86·5	B	+ 2·2	0	40·8
			V. Polynesian crania (19)					
53	XXVIII. A. 18	1715	1227	71·5	D	− 4·8	−2·5	35·4
54	XXVIII. A. 24	1736	1168	67·2	D	− 2·4	−2·5	32·7
55	XXVIII. A. 29	1686	1224	72·5	D	− 3·6	+1·5	32·8
56	XXVIII. A. 30	1700	1221	71·8	D	0	+3·0	37·0
57	XXVIII. A. 32	1878	1380	73·4	D	− 7·6	−1·0	39·5

Serial no.	Catalogue no.	Length	Width	Cranial index	Class	Relation of centre of lower border of internal auditory meatus: Horizontal to external auditory meatus (mm.)	Vertical to external auditory meatus (mm.)	Mesial to posterior root of zygoma (mm.)
			V. Polynesian crania (19) (*cont.*)					
58	XXVIII. A. 34	1785	1147	64·2	D	− 6·5	−1·0	33·8
59	XXVIII. A. 35	1774	1274	71·8	D	+ 3·5	−1·0	39·6
60	XXVIII. B. 2	1882	1257	66·7	D	− 1·9	+2·5	35·0
61	XXVIII. C. 28	1872	1243	66·3	D	− 7·1	+0·5	37·5
62	XXVIII. C. 32	1786	1190	66·6	D	0	−1·0	35·3
63	XXVIII. C. 33	1807	1241	68·6	D	0	−1·5	35·1
64	XXVIII. F. 45	1725	1470	85·2	B	+ 7·3	+3·0	43·0
65	XXVIII. G. 1	1722	1217	72·9	D	+ 1·6	+1·0	38·6
66	XXVIII. G. 5	1872	1370	73·1	D	− 0·9	+6·0	36·5
67	XXVIII. G. 17	1890	1418	75·0	M (D)	0	+3·0	39·6
68	XXVIII. H. 4	1708	1239	72·5	D	+ 1·5	0	36·5
69	XXVIII. H. 12	1954	1310	67·0	D	+ 4·0	−0·5	36·2
70	XXVIII. H. 17	1767	1189	67·2	D	− 4·1	+1·0	36·6
83	XXXI. A. 27	1877	1350	71·9	D	− 1·6	+0·5	41·3
			VI. Australian crania (23)					
71	XXIX. A. 10	1852	1285	69·3	D	− 6·2	−3·0	34·8
72	XXIX. A. 11	1943	1287	66·2	D	0	+0·5	38·1
73	XXIX. A. 14	1864	1258	67·4	D	−11·6	+4·0	34·8
74	XXIX. B. 3	1753	1246	71·0	D	− 6·5	−1·5	34·5
75	XXIX. B. 5	1937	1252	64·6	D	− 8·8	+2·5	36·5
76	XXIX. B. 12	1968	1255	63·7	D	− 1·3	−1·0	39·6
77	XXIX. C. 10	1875	1203	64·1	D	− 8·0	−1·5	34·8
78	XXIX. C. 18	1787	1260	70·5	D	− 3·8	+2·5	36·6
79	XXIX. D. 3	1652	1218	73·7	D	− 2·8	−1·0	33·9
80	XXIX. G. 17	1721	1229	71·4	D	− 5·5	−1·0	34·7
81	XXX. 2	1836	1359	74·0	D	− 6·2	+2·5	36·7
82	XXX. 5	1766	1295	73·3	D	0	+3·0	37·4
96	XXIX. D. 17	1748	1277	73·0	D	− 7·5	−6·0	36·1
97	XXIX. D. 18	1765	1269	71·8	D	+ 4·0	+2·0	38·7
98	XXIX. D. 20	1839	1215	66·0	D	0	+4·0	36·5
99	XXIX. D. 29	1821	1267	69·5	D	− 5·5	−3·0	37·8
100	XXIX. D. 43	1882	1337	71·0	D	− 7·5	−0·5	37·1
101	XXIX. D. 45	1831	1213	66·2	D	− 6·3	−3·0	36·0
102	XXIX. D. 61	1783	1198	67·1	D	− 7·7	−2·0	35·4
103	XXIX. D. 66	1816	1278	70·3	D	− 4·6	−6·0	38·7
104	XXIX. D. 73	1744	1204	69·0	D	−11·3	−3·0	34·1
105	XXX. 1	1796	1287	71·6	D	− 1·6	−6·0	38·0
107	XXIX. D. 28	1794	1265	70·5	D	− 8·0	+1·0	36·2
			VII. Amerindian crania (9)					
84	XXXII. A. 1	1625	1579	97·1	B	− 6·3	+2·5	43·1
85	XXXII. A. 3	1738	1526	87·7	B	− 6·5	+3·5	40·1
86	XXXIII. A. 3	1637	1455	88·8	B	− 1·4	+1·5	41·3
87	XXXIII. A. 6	1546	1421	91·9	B	− 4·7	+1·5	35·7
88	XXXIII. A. 26	2024	1289	63·1	D	+ 1·0	+1·0	38·9
89	XXXIII. A. 33	1575	1331	84·5	B	− 7·5	+0·5	38·0
90	XXXIII. B. 4	1460	1554	106·4	B	− 5·4	+7·0	38·8
91	XXXIII. C. 6	1922	1485	77·2	M (D)	+ 7·4	+6·5	46·5
106	XXXIII. C. 4	1833	1293	70·5	D	− 2·6	0	38·8
			VIII. Microcephalic crania (4)					
92	XXXV. A. 1	1740	1202	69·0	D	−10·4	+2·5	34·2
93	XXXV. A. 2	1584	1240	78·2	M (B)	− 9·5	−1·0	31·5
94	XXXV. A. 6	1495	1024	68·4	D	− 6·0	−5·5	28·1
95	XXXV. A. 7	1302	915	70·2	D	−11·0	−5·0	25·9

CRANIAL INDEX DIFFERENTIATION

Again dividing these 107 crania according to their indices the following results are obtained:

Dolichocephalics

(*a*) Relation to the highest point of the external auditory meatus.

(i) Vertical

+	−	0·0
42 = 105·5	39 = 81·0	5 = 0·0
∴ 1 = 2·5	∴ 1 = 2·07	

$$+ = 2{\cdot}5$$
$$- = 2{\cdot}07$$
$$\text{Diff.} = +0{\cdot}43$$

(ii) Horizontal:

+	−	0·0
13 = 51·0	59 = 352·7	14 = 0·0
∴ 1 = 3·9	∴ 1 = 5·9	

$$- = 5{\cdot}9$$
$$+ = 3{\cdot}9$$
$$\text{Diff.} = -2{\cdot}0$$

(*b*) Relation to the posterior root of the zygoma.

$$86 = 3135{\cdot}5$$
$$\therefore\ 1 = 36{\cdot}4$$

That is to say, in Dolichocephalic crania the centre of the lower border of the internal auditory meatus lies 0·43 mm. superior and 2·0 mm. posterior to the highest point of the external auditory meatus, and 36·4 mm. mesial to the posterior root of the zygoma immediately above the highest point of the external auditory meatus.

Brachycephalics

(*a*) Relation to the highest point of the external auditory meatus.

(i) Vertical:

+	−	0·0
13 = 36·5	1 = 3·5	3 = 0·0
∴ 1 = 2·8		

$$- = 3{\cdot}5$$
$$+ = 2{\cdot}8$$
$$\text{Diff.} = -0{\cdot}7$$

(ii) Horizontal:

+	−	0·0
3 = 13·0	14 = 95·1	0 = 0·0
∴ 1 = 4·3	∴ 1 = 6·8 nearly	

$$- = 6{\cdot}8$$
$$+ = 4{\cdot}3$$
$$\text{Diff.} = -2{\cdot}5$$

(*b*) Relation to the posterior root of the zygoma.

$$17 = 640{\cdot}2$$
$$\therefore\ 1 = 37{\cdot}6$$

That is to say, in Brachycephalic crania the centre of the lower border of the internal auditory meatus lies 0·7 mm. inferior and 2·5 mm. posterior to the highest point of the external auditory meatus, and 37·6 mm. mesial to the posterior root of the zygoma immediately above the highest point of the external auditory meatus.

Microcephalics.

(*a*) Relation to the highest point of the external auditory meatus.

(i) Vertical:

+	−	0·0
1=2·5	3=11·5	0=0·0
	∴ 1= 3·83	
	− = 3·83	
	+ = 2·5	
	Diff. = −1·33	

(ii) Horizontal:

+	−	0·0
0=+	4=36·9	0=0·0
	∴ 1= 9·22	
	− = 9·22	
	+ = 0·00	
	Diff. = −9·22	

(*b*) Relation to the posterior root of the zygoma.

4=119·7
∴ 1= 29·9

That is to say, in Microcephalic crania the centre of the lower border of the internal auditory meatus lies 1·33 mm. inferior and 9·22 mm. posterior to the highest point of the external auditory meatus, and 29·9 mm. mesial to the posterior root of the zygoma immediately above the highest point of the external auditory meatus.

Summing up the series but eliminating the microcephalics:

(*a*) Relation to the highest point of the external auditory meatus.

	Vertical			Horizontal		
	+	−	0·0	+	−	0·0
Dolicho.	42=105·5	39=81·0	5=0·0	13=51·0	59=352·7	14=0·0
Brachy.	13= 36·5	1= 3·5	3=0·0	3=13·0	14= 95·1	0=0·0
	55=142·0	40=84·5	8=0·0	16=64·0	73=447·8	14=0·0
	∴ 1= 2·6	∴ 1= 2·1		∴ 1= 4·0	∴ 1= 6·1	
		+ = 2·6			− = 6·1	
		− = 2·1			+ = 4·0	
		Diff. = +0·5			Diff. = −2·1	

(*b*) Relation to the posterior root of the zygoma.

86=3135·5
17= 640·2
∴ 103=3775·7
∴ 1= 36·6

That is to say, the centre of the lower border of the internal auditory meatus lies 0·5 mm. superior and 2·1 mm. posterior to the highest point of the external auditory meatus and 36·6 mm. mesial to the posterior root of the zygoma immediately above the highest point of the external auditory meatus.

The above is a part of some work done in comparative anatomy while on study leave. The whole of the work has been done in the Department of Anatomy of the University of Edinburgh, and my most grateful thanks are due to Prof. Arthur Robinson and to the University not only for permission to use the material but for more than kindly help and valuable criticism and instruction.

I would also like to express my thanks to Miss Murdoch, craniographist to Prof. Robinson, for initial help in mastering the use of the craniograph.

THE EMISSARY FORAMINA OF THE CRANIUM IN MAN AND THE ANTHROPOIDS

By G. I. BOYD, M.D., F.R.C.S. (Edin.)

Formerly Demonstrator of Anatomy, University of Edinburgh

The emissary foramina in Man have received attention from many authors; but usually only one foramen has been described by each author, and only an approximate estimate of its size has been made. The comparative anatomy of these formina has received little attention and their anthropological aspect even less.

In view of the gaps in our knowledge of their comparative anatomy, and because they are in some cases the paths by which infection is carried to the cranial cavity, I thought the subject worthy of further investigation—the results of which were made the substance of a thesis for the degree of M.D. in the University of Edinburgh, 1929, and are here briefly summarised.

I systematically examined 1500 crania in the Anatomical Museum of the University. I supplemented what I found in these dried skulls by observations made on the material which passed through the dissecting room, and on the crania of fresh foetuses injected with blue gelatine. To complete the anthropological survey, I compared the foramina in human crania with those of 124 crania of anthropoid apes. My statements on the comparative anatomy are based on the examination of these and of 160 skulls of other Mammals.

Emissary veins are the veins that connect the extracranial venous system with the blood sinuses and meningeal veins. But all the foramina that transmit emissary veins are not called emissary foramina. In ordinary usage the term is restricted to the following pairs—parietal ramen, mastoid foramen, condyloid foramen and foramen of Vesalius. The term could include also an occasional median foramen in the occipital bone, and the foramen caecum, which is commonly described as the channel for an emissary vein.

For measurement I used graduated wires, 1, 1·5, 2, 2·5, 3 and 4 mm. in diameter, while every aperture below 1 mm. which admitted a hair was recorded as 0·5 mm. The wires were pliable to a certain extent, so that up to a point they could be adapted to a curved canal, but in many cases I found difficulty in coming to a decision in regard to the bore of the canal, owing to its sinuosity, and also because sometimes the external aperture was quite large, while the lumen narrowed down considerably. The difficulty was greatest in the condyloid foramen, which is a canal with a right-angled bend, and in the mastoid foramen, which may be a long, much curved bony canal, intimately associated with the posterior temporal diploic vein—so sinuous that it is impossible to pass a probe—and one is left in doubt as to whether there is

a complete emissary foramen or not. In some cases what is ordinarily an emissary foramen was a mere pit or a blind canal; in these cases, together with those too narrow to transmit a hair, the foramina were recorded as absent. A laryngeal mirror was used for noting the transmission of the hair in unsectioned skulls.

THE PARIETAL FORAMEN

The parietal foramen varies in position within fairly well-defined limits. It is present on both sides in 19·9 per cent. of skulls, is absent on both sides in 39·6 per cent. A single foramen is commoner on the right side (20·7 per cent.) than on the left (15·2 per cent.). A median (sagittal) foramen was present alone in 4·6 per cent. of cases, and accompanied by one or other parietal foramen in 1·3 per cent., making a total of 5·9 per cent. Parietal foramina were multiple on one or both sides in 2·5 per cent. of cases.

The foramina are practically equal in size on the two sides. In about half the cases the average bore is 0·5 mm. or under. In only 7 per cent. is the bore 1·5 mm. or over. In the rest it is 1 mm.

The parietal foramina in Australian and New Zealand skulls are larger than in the skulls of other races; and a median position is more common, especially in comparison with White races. Le Double (21) points out that the parietal foramina are more frequently absent in White races than in Primitive races such as Australians, and my figures confirm this (48·4 and 35 per cent. respectively).

Abnormally large parietal foramina

A pair of abnormally large parietal foramina were found in one skull-cap (Os.G.a.1, Y.169). Both foramina are round, the left 9 mm. in diameter, and the right 15 mm. (Plate I, fig. 1). They are joined by a suture visible on the external aspect of the calvaria, and the edges are 10 mm. apart; and a point midway between the two foramina is 30 mm. from the lambda. Internally, the groove for the sagittal sinus runs to the right of the median plane, close to the medial margin of the right foramen. The edges of the foramina are bevelled at the expense of the inner table, hardly at all of the outer. The foramina are closed by a fibrous membrane which belongs both to the dura mater and to the pericranium. The radiogram (Plate I, fig. 2) shows the nature of the openings in the bone, and the suture joining them, which represents the notch or fissure found in most parietal bones at birth (Paterson and Lovegrove (31)).

Pamperl (30), writing in 1919, stated that only 36 skulls showing a pair of abnormally large parietal foramina had been recorded to date, and that the abnormality had been observed only five times during life. The first case described during life was recorded by Greig (10) in 1892; and in 1917 (11) he described a similar peculiarity in the brother of his first case, though mention of this second case was omitted from Pamperl's list. Greig quotes other cases of familial defect recorded by Maciesza (23) and Symmers (37). Two additional (unrelated) cases have since been described by Cave (44), and one by Stibbe (45).

Another skull (XXIX. D. 31 Australian—presumed to be male) shows an abnormally large unilateral parietal foramen (Plate I, fig. 3). The foramen is on the left side. It is oval, with the long axis vertical instead of horizontal. Its margins are smooth and are bevelled at the expense of the outer table and to some extent of the inner also. It measures 7 by 4 mm. and is close to the sagittal suture, which actually forms its medial boundary for 2 mm. anteriorly. Its mid-point is 24 mm. in front of the lambda. Internally, a well-marked groove passes backwards from the foramen to the right side of the occipital protuberance, where it turns to the right to end in the right transverse sulcus. The sagittal sulcus runs backwards to the foramen and divides into two portions, one of which ends at the foramen, while the other runs past the left side of the foramen and onwards to the protuberance, where it bends to the left. This posterior portion of the sagittal sulcus is separated by a ridge from the groove that leads backwards from the foramen. (The skull was in too friable a condition to be sectioned, so that photographs of the interior were not obtainable.)

Examples of a large unilateral parietal foramen have been described by Humphrey (17), by Derry (6), by Lancisci and Walter (quoted by Greig (14)). Those described by Humphrey and by Derry are associated with flattening and thinning of both parietal bones. An allied condition—enlargement of one of a pair—has been described by Le Double (21), by Gruber (16) and by Wrany (quoted by Pamperl (30)).

Relation of enlarged parietal foramina to emissary veins

In most of the recorded cases there is no evidence that an enlarged foramen transmitted a large vein. Small vascular grooves have been found at the edges of these foramina, but a large groove has seldom been seen; and a large vein would presumably have left its mark on the bone near the foramen, as is the case in the Australian skull previously mentioned. Further, in several cases an obturating membrane was found in the foramen. In the two specimens recorded by Symmers (37) and by Maclagan and Turner (26), (39), several minute vessels had perforated the membrane, and in that recorded by Bialnicki and cited by Maciesza (23), the membrane was whole, as it was also in the skull-cap described here. The suggestion is therefore that a large parietal foramen is usually not an aperture made for the transmission of a vessel but is due to defective ossification, and that is supported, among other things, by the fact that in some skulls the large foramen is associated with thinness of the parietal bone.

THE MASTOID FORAMEN

The mastoid foramen is present on both sides in 34·4 per cent., absent on both sides in 31·9 per cent., and present on one side only in nearly equal proportions (16·1 per cent. on the right, and 17·6 per cent. on the left). In 10·3 per cent. of skulls, the foramina were multiple on one or both sides, more commonly on the right side, in the proportion 76 : 56.

The bore of the foramen is about 1 mm. In about 10 per cent. of cases it is over 2 mm.; rarely is it 4 or 5 mm. As a rule, the right foramen is larger than the left and more often multiple—a fact noted by Sperino (35) and Le Double (21).

The mastoid foramen is smaller and less commonly present (57 per cent.) in Australians than in other races, especially when compared with White races.

Abnormally large mastoid foramina

A Scottish male skull (I.B. 177) shows a large left mastoid foramen, having two external openings, through both of which the mastoid-occipital suture passes. The upper external opening is 8 mm. horizontally by 5 mm.; the lower from 1·5 to 2 mm. The internal opening measures 13 mm. horizontally by 4 mm. and is just in front of the suture. The left transverse sulcus ends at the enlarged mastoid foramen. The left jugular foramen is small and receives the inferior petrosal sulcus, which is fairly large. The jugular fossa is absent.

Gruber was the first to describe the condition. In 1875 (15) he described a tortuous right mastoid canal, the inner orifice measuring 8 mm. by 6 mm., the outer 15 mm. by 9 mm. Both jugular foramina were unusually small. In 1903, Laidlaw (19) described an isolated left temporal bone of an Egyptian skull, which showed (1) absence of the internal auditory meatus, and (2) absence of the jugular fossa, with partial absence of the transverse sulcus and the presence of a large mastoid foramen. The transverse sulcus ended at the mastoid foramen. Le Double (21) mentions that he has a skull with a mastoid foramen on each side measuring 20 mm. in diameter. Meyer (27), in 1914, described a skull with a large right mastoid foramen, the outer opening, oval in shape, measuring 8 mm., the inner only 6 mm.; the jugular foramen was of the usual size. He also quotes a case described by Merkel, with a mastoid foramen large enough to admit the tip of the little finger. Merkel ascribed the condition to yielding of the base of the skull due to rickets, with encroachment on the jugular foramen, and compensatory widening of the mastoid foramen. In 1925 Cheatle (3) described two cases. In one of them both mastoid foramina were abnormally large, the left measuring about 10 mm., and the right about 6 mm.; the lower parts of both the transverse sulci were absent, the jugular foramina being small and the jugular fossae absent. In the other the left transverse sulcus ended half an inch from the jugular foramen, and turned abruptly through a mastoid foramen nearly half an inch in diameter. On the same side the jugular foramen was small and the jugular fossa absent. The other mastoid foramen was one-eighth of an inch, and the jugular fossa present. Malacre and Budde, quoted by Braun (43), each describe a skull with large mastoid foramina. In both skulls the right mastoid foramen measured 10 mm., and the left was smaller. The transverse sulci were of normal width but ended at the mastoid foramina. The jugular foramina were small. In Greig's oxycephalic skull (13), the base being narrow, the jugular foramina were small and the jugular fossae absent, and the blood was drained away through enlarged mastoid foramina and by adventitious foramina.

The aetiology of a large mastoid foramen is obscure except in the pathological cases cited. Cheatle (3) suggests that it is an atavistic condition; but that is unlikely, as the foramen is more constant in Man than in apes. It may be associated with abnormal development of the transverse sinus. The horizontal and sigmoid parts of that sinus are formed at different times; if the sigmoid part fails to develop, the horizontal part will leave the skull through an enlarged mastoid foramen.

THE CONDYLOID FORAMEN

The condyloid foramen has received little attention in the literature. It is present on both sides in 46·6 per cent. of skulls—a higher percentage than in the case of any other foramen. It is absent on both sides in only 23·1 per cent. A unilateral condyloid foramen is present rather more often on the right side than on the left (16·5 and 13·8 per cent.).

It is the largest of the emissary foramina, its bore varying from 1 to 2 mm. It is less than 1 mm. in only 10 per cent. of cases, and in 15 per cent. is more than 2 mm. It is somewhat wider on the right side, in correspondence with the greater size of the right transverse sinus—a fact noted also by Sperino (35) and Le Double (21). In Australian skulls it is smaller than in other races and is less often present in the proportion of 67 : 77.

FORAMEN OF VESALIUS

The foramen of vesalius has received even less attention than the condyloid. It is present on both sides in only 14·7 per cent. of skulls, and absent on both sides in 63·5 per cent. It is present on the right side only in 10·6 per cent., and on the left side only in 11·2 per cent. In one skull the foramen was double. Though it is often absent, its place may be taken by two or more diploic channels opening independently on the interior and exterior of the skull.

In 65 per cent. of cases the foramen was 0·5 mm., usually just admitting a hair. In most of the others it was 1 mm. In only 5 per cent. of cases was it over 1 mm., 2 mm. in three cases and 2·5 in one.

EMISSARY FORAMINA AS A WHOLE

Considering the emissary foramina as a whole, I found no difference in the age or sex incidence. The condyloid foramen is that most frequently present, and is the largest; yet that is the one foramen which is less frequent in Australians, uncommon in anthropoids and absent in all other animals. The Australians are believed, on various grounds, to stand low in the anthropological scale, and the similarity of the distribution of their emissary foramina and those of Simians (in contrast to the arrangement found in White races), suggests that these features are to be considered "Simian characters."

A noteworthy feature is the almost unvarying presence of one or more emissary foramina. In only 3·5 per cent. of the human skulls were there no

emissary foramina, and even in the Australians, with their Simian tendency, they were absent in only 7·7 per cent.

It must be remembered that diploic veins by their communications with the intra- and extracranial venous systems may indirectly become emissary channels. I was struck by the close association of the emissary and diploic veins in the course of my investigations, and Jefferson and Stewart (18) also comment on this, while Deaver (5) refers to its importance in the spread of infection. This association was confirmed by the examination of the emissary and diploic channels exposed in detached parietal, temporal and occipital bones (some of them injected); but the communications varied in degree and were not always present.

FORAMINA NOT USUALLY PRESENT

Frontal bone

The foramen caecum was described by the older anatomists as a blind pit in the frontal bone, as its name implies, but modern textbooks, almost without exception, give the impression that it is usual for the canal to be patent and to be traversed by a vein joining the superior sagittal sinus with the veins of the nose (1, 2, 4, 9, 32, 33, 38, 43). I have found that this is quite the exception and I am supported in this finding by Le Double (21). The size is very variable. In over a score of bodies in the dissecting room I found a root-like process of dura mater filling the pit. In no case was I able to pass a hair into it from the lumen of the superior sagittal sinus.

The interior was accessible in 212 of the skulls. In only 3 of them (1·4 per cent.) did I find a definite canal traversing the bone. In one, the canal was 3 cm. in length, very narrow, just admitting a hair, opening on to the outer aspect of the left nasal bone just above the vascular foramen normally present. In another, a fine hair passed through the foramen caecum and emerged on the outer aspect of the right nasal bone. In the third, the foramen caecum admitted a fine hair which passed down in a canal in the septum between the frontal sinuses, and opened on the roof of the nose close to the left side of the septum (the entire canal being in the frontal bone).

An abnormal canal piercing the squamous part of the frontal bone is present in a female skull (about 25 years of age). It is 17 mm. in length and somewhat sinuous, opening internally into the sagittal groove, 20 mm. above the foramen caecum, while the external opening is 7 mm. to the right of the middle line and 5 mm. above the supra-orbital margin (Plate I, fig. 4). At each orifice it admits a probe of 1·5 mm., but such an instrument cannot be passed on account of the sinuosity. The sagittal groove tapers off gradually, and the foramen caecum is blind.

Emissary canals in the frontal bone are referred to by Greig in his skulls showing hypertelorism and oxycephaly (12, 13), by Nettleship in a living subject (28) and by Quain (33).

Occipital bone

An emissary foramen in the region of the inion, close to or in the middle line, and opening internally, was present in 1·6 per cent. skulls and was always single. In 10 cases it was 0·5 mm. in size, in 13 cases 1 mm., while in one skull the canal was 2 mm. externally and had two internal openings each 1 mm.

The oxycephalic skull described by Greig (13) shows a large occipital foramen, 10 mm. in bore, mastoid foramina larger than usual and a right squamosal foramen. Reuben and Cleaver (34) described a large occipital emissary vein in the living subject—a boy with oxycephaly.

Temporal bone

Postglenoid or squamosal foramen (foramen jugulare spurium of Luschka)

I have found this foramen in 8 skulls (0·6 per cent.)—at the lateral end of the petro-tympanic fissure in two of them (postglenoid foramen), just above the root of the zygoma in the other six (squamosal foramen). It gives exit to the petrosquamosal sinus. The bore was 0·5 mm., except in one which was 1·5 mm. throughout.

Le Double (21) discusses the frequency of this foramen and points out the normal occurrence of diploic openings at the site of the foramen and at the posterior part of the mandibular fossa—a fact which I noted many times both in human and animal skulls. Braun (43) quotes Cheatle, who found a persistent spurious jugular foramen in 23 skulls out of 2585 (1 per cent.)—14 postglenoid and 9 squamosal. Streit, also quoted by Braun, describes the foramen. The squamosal foramen in Greig's oxycephalic skull (13) has already been mentioned.

The "foramen jugulare spurium" was first described by Luschka, who believed that it drained the blood from the embryonic skull into the external jugular vein; but Mall (24) points out that this vein is formed after the internal jugular, and that Luschka's conclusion in this respect was erroneous.

Streeter (36) states that "the foramen jugulare spurium corresponds to the persistent otic portion of the primary head vein" (vena capitis lateralis of Mall) "which in the foetus drains into the internal jugular vein," though it may later form a secondary communication with the external jugular vein. This otic portion, however, runs backwards from the cavernous sinus, to be associated with the facial nerve, presumably at the genu, whereas the petrosquamous sinus runs forwards along the petrosquamous suture from the lateral end of the horizontal part of the transverse sinus, above and lateral to the ear, to end at the postglenoid or squamosal foramen and usually has no connection with the cavernous sinus. I have no information concerning the embryology of the temporal canal in animals, which is the homologue of the petrosquamous sinus in Man. No embryological explanation that seems adequate has been given for a postglenoid foramen in the human; but it is

probable that the foramen, along with the petrosquamous sulcus, is a vestigial relic of the temporal canal, which is constant in some animals and becomes increasingly rare as we ascend the Primate scale.

EMISSARY FORAMINA IN LOWER ANIMALS

I have found no mention of the foramen caecum or condyloid foramen in the literature.

Paterson and Lovegrove (31) found the parietal foramen only in the bear, ox and leopard. Le Double (21) did not find it in Aves, Herbivora, Carnivora, Rodents or any monkey, but quotes Ranke, who found it in orangs and gibbons. Le Double discusses fully the postglenoid or squamosal foramen and the temporal canal, cataloguing the species in which it is present; and he refers briefly to the mastoid foramen. Cheatle (3) states that in the lemur, dog and horse the lower part of the transverse sinus is absent and the mastoid foramen has a share in emptying the transverse sinus, and may be very large.

Table of percentage comparison of Man and anthropoids

	Foramina present on one or both sides			
Skulls examined	Parietal	Mastoid	Condyloid	Postglenoid
1478 Man	60·5	68	77	0·5
124 Anthropoids	8	41	5·6	27·4
50 Simiidae	18	26	6	2
18 Gorillas	33	5	0	0
14 Chimpanzees	14	0	14	0
14 Orang-Utans	7	78	7	7
4 Gibbons	0	25	0	0
74 Other monkeys	1	51	5	43

In the present investigation, the accompanying table gives the relative frequency of the emissary foramina in Man and Anthropoids. The *foramen caecum* was never patent (except in the few cases already mentioned in human skulls).

The *parietal foramen*, when present, was always single. It was situated in the median plane, except in two skulls, once on the right and once on the left. It was more common in Simians, being present in 18 per cent., while it was present only once in 74 skulls of the other monkeys. It was not present in any of the 4 gibbons examined. It occurred with increasing frequency in orangs, chimpanzees and gorillas in that order (and, in addition to the six gorilla skulls with complete parietal foramina, four showed incomplete parietal openings).

The *mastoid foramen* was present in 41 per cent. of Anthropoids. In the Simians it was present only in 26 per cent., and this figure is due to its common occurrence in orangs (78 per cent.); in the other monkeys it occurred in 51 per cent. The foramen was absent in chimpanzees and present only once in the gorillas.

The *condyloid foramen* was present only in 5·6 per cent. of Anthropoids (6 per cent. in Simians and 5 per cent. in the other monkeys).

The *postglenoid foramen* occurred in 27·4 per cent. of Anthropoids, but among Simians was present only in one orang (on both sides), though incomplete foramina were noted in four other orang skulls.

Among the Simians, many skulls showed no foramina at all—11 out of 18 gorillas, 8 out of 14 chimpanzees and 3 out of 4 gibbons, but only 3 out of 14 orangs. Old World and New World monkeys showed no difference when compared. In 4 lemurs examined, two had a pair of mastoid foramina and a pair of postglenoid foramina, while the other two had a pair of postglenoid foramina alone. The postglenoid foramen in the lemur was larger than the jugular foramen.

The animals examined, other than Primates, were 75 Carnivora, 75 Ungulates, 7 Rodents and 3 Proboscidae. In them, a single parietal foramen was found in the Ungulates alone—twice in the ox, twice in the camel and once in a rhinoceros. (In the 6 hippopotami, doubtful apertures were present in the parietal bone.) The condyloid foramen was not found.

The postglenoid foramen was absent in Rodents and Proboscidae; among Carnivora, it was absent in all Felidae and Pinnipedia, and present in all Canidae and bears (except the one badger examined); it was present in all the Ungulates except the Suidae, Hippopotamidae and the two rhinoceros skulls examined. The foramen was largest in the Cervidae, in many of which it was merely one of a series of terminal openings to the temporal canal, the others being squamosal. (Sometimes that canal ended in a single squamosal foramen.) In the dog and bear, the postglenoid foramen is moderate in size, for part of the blood from the cranial cavity leaves by the jugular foramen. Five dog skulls were sectioned and one skull injected with the soft parts *in situ*. The tentorium cerebelli is partly ossified at the periphery, and the transverse sulcus converted into a bony canal, which begins at the internal occipital protuberance, and runs forwards to the mastoid angle of the parietal bone. Instead of bending downwards, as in the human skull, the main portion of the channel runs forwards and traverses the temporal bone, in the line of the petrosquamous suture, and then turns downwards and opens at the postglenoid foramen, between the petrous and squamous temporal, behind the mandibular fossa, and in front of the external auditory meatus, separating the meatus from the postglenoid tubercle. This channel is called the temporal canal. It corresponds to the petrosquamous sulcus in Man (which resembles it when converted into the canal of Verga, by being roofed over). In the dog there is a small aperture in the lower wall of the temporal canal, which is continuous with a sigmoid groove that runs down to the jugular foramen.

The mastoid foramen is present in all those animals which have a temporal canal and postglenoid foramen. It was absent, however, in the one giraffe, in an ox, a sheep and a few deer; it was present in two Suidae, and three out of

six hippopotami and the rhinoceros. It was completely absent in all Rodents, Proboscidae, Felidae and Pinnipedia. Though sometimes large in the horse, it was never large in the dog, and in both was always smaller than the postglenoid foramen.

COMPARISON OF MAN AND LOWER ANIMALS

On the whole, the facts stated show that emissary foramina are less common in lower animals than in Man. In the human skull all three pairs of foramina may be present (parietal, mastoid and condyloid); in lower animals there may be two pairs of foramina, but usually there is only one (single or paired); and in Felidae, Proboscidae and Rodents there are no emissary foramina at all.

The *parietal foramen* is rarely present in lower animals except in Simians, which stand next to Man in the zoological scale, and it is always single. It is most frequent in the gorilla, being present in 33 per cent. of cases, while in Man it is present in 60 per cent. of cases.

The *condyloid foramen*, which is the largest and most constant (77 per cent.) of all the foramina in Man, is even more infrequent in lower animals than the parietal foramen, being found in only 5·6 per cent. of Anthropoid crania, and not at all in other Mammals.

The *mastoid foramen*, present in 68 per cent. of human skulls, varies greatly in frequency in the different species of lower animals. It is less frequent (41 per cent.) in the Anthropoids than in Man, and among them it is least frequent in Simians. It is absent in some animals, but is very constantly present in animals with a temporal canal, such as dogs, bears, and most Ungulates.

The *postglenoid foramen*, an aperture rarely met with in Man (0·5 per cent.), is uncommon in Simians also (2 per cent.), but is normally present in many other animals—in 43 per cent. of other monkeys, and very constant in dogs, bears and most Ungulates. In these animals the jugular foramen is small and a greater or less part of the venous blood is conveyed through the postglenoid foramen, the proportion varying in the different species.

In Mammals below Anthropoids, two different types are found: (1) those with no emissary foramina at all, the jugular foramen alone draining the cranial cavity; and (2) those which have a temporal canal, postglenoid foramen and accompanying mastoid foramen. Anthropoids provide the transition stage from both these types to the drainage system found in Man, the Simians approximating the human system, the gorilla in the direction of parietal foramina, the orang in the direction of mastoid foramina, and possibly the chimpanzee in the direction of parietal and condyloid foramina. On the other hand, as mentioned previously, the skulls of certain races of Man show Simian characters, in respect of emissary foramina.

CLINICAL ASPECT OF THE EMISSARY FORAMINA

Infection of the cranial cavity may pass by lymphatics, by sheaths of cranial nerves, by emissary veins and by direct continuity of spread through bone. Piersol (32) quotes the well-known aphorism of Treves, "If there were no emissary veins, injuries and diseases of the scalp would lose half their seriousness."

In spite of the fact that spread of infection is referred to in textbooks as a not uncommon occurrence, I have found only a few references to specific clinical instances.

Sinus-thrombophlebitis occurs most frequently in the transverse sinus and is invariably otitic in origin; but Friedman and Greenfield (8) found at operation a mastoid emissary vein, three-eighths of an inch in diameter, separately and directly the seat of septic thrombosis resulting from infected mastoid air-cells, without implication of the transverse sinus. Turner and Reynolds have made a special study of paths of infection to the cavernous sinus from the vestibule of the nose (40), nasal cavities and accessory air sinuses (41). Otto (29) records a case where infection spread from a carbuncle of the neck to the cavernous sinus by the occipital vein, mastoid emissary vein and superior petrosal sinus. Langworthy (20) mentions a case reported to him by Patton, of a cavernous sinus thrombosis secondary to a boil on the neck, and another case secondary to "an infection of the neck." In nearly all cases of intracranial complications following infections of the face, the spread probably occurs by way of the ophthalmic veins to the cavernous sinus, and only rarely to the superior sagittal sinus by way of the foramen caecum. The subaponeurotic space, being traversed by the parietal emissary vein, has been referred to as the "danger area of the scalp," but whether this idea is supported by clinical experience or is merely an anatomical inference, I have not been able to discover. This path of infection is open in the majority of people, but in a considerable number the parietal foramina are absent, so that the risks would be lessened in their case. This absence may account for the fact that in some cases of severe sepsis of the scalp no intracranial complications follow. Osteomyelitis of the calvaria, meningitis and cerebral abscess may arise from infection spreading along the diploic, meningeal and cerebral veins which communicate with the emissary veins.

The emissary veins are important agents in equalising intracranial pressure, and in conditions of cerebral congestion it would appear that they can act as safety valves. But the explanation that epistaxis is due to escape of blood by way of the foramen caecum seems untenable in view of the infrequency of the foramen. The application of leeches behind the ear and at the back of the neck is an ancient therapeutic measure which probably depends for its efficacy on the proximity of the mastoid and condyloid foramina. The adventitious foramina noted in oxycephalic skulls, which are characterised by narrowness

of the base and absence of diploe, may be compensatory for the small jugular foramen and absent diploic channels.

In cases of intracranial tumour, no enlargement of the emissary foramina has been reported, but there is sometimes marked vascularity of the scalp and skull immediately over the tumour, especially in endotheliomata (Elsberg and Schwartz (7)). Lewald (22) and Jefferson and Stewart (18) point out that so-called enlarged unilateral diploic veins may occur in normal people, especially in the later decades of life, and emphasise the danger of operating, when the diagnosis of cerebral tumour has been made on radiological evidence without sufficient clinical evidence. Dott (42) has found radiographic appearances helpful in many cases. He pointed out that the increased vascularity was in no way due to venous obstruction, but affected all the tissues equally in response to the growth requirements of the tumour. In one case where an adventitious foramen had formed for the passage of vessels, the arteries were more prominent than the veins, while in another case the parietal foramen directly overlying the tumour was found at operation not to be enlarged.

In clinical examination, the possibility of enlarged parietal foramina must be remembered and differentiated from other deficiencies in the skull-cap. In certain operations also the possibility of enlarged emissary veins has to be kept in mind. A case is recorded by M'Kenzie (25) where an enlarged mastoid vein complicated an operation. In the approach to the cerebellar fossa, serious haemorrhage may occur at the condyloid emissary foramina, but there is rarely any necessity to remove bone as far forwards. Bleeding at the occipital protuberance, however, tends to diminish as the operation proceeds (Jefferson and Stewart (18)).

SUMMARY AND CONCLUSIONS

1. The frequency and size of the parietal, mastoid, condyloid emissary foramina and the foramen of Vesalius is given.

2. There are no age or sex differences in these foramina.

3. There is a marked contrast between Australian and other races, especially the White races, in the distribution and size of the emissary foramina.

4. The foramen caecum is rarely present, probably in only 1·4 per cent. of skulls. An occipital emissary foramen was present in 1·7 per cent. Cases are quoted where it was of considerable size. A postglenoid or squamosal foramen was found in 0·5 per cent. skulls. It is constantly present in certain animals, but is rarely found in Simians.

5. Differences in the arrangement of the emissary foramina in the various animals are noted. The Simians appear to occupy an intermediate position between the other Anthropoids and Man, resembling Australian skulls in the particulars noted as "Simian characters." The emissary foramina are, on the whole, less common in lower animals than in Man, and in certain species are altogether absent.

6. Abnormally large parietal foramina may be met with. They are probably due to a defect in the ossification of the parietal bones and are not usually associated with an enlarged emissary vein.

7. Abnormally large mastoid foramina may be met with, associated with an enlarged emissary vein, which may take the place of the sigmoid part of the transverse sinus. One such case is recorded; other examples are cited from the literature.

8. There is an important relationship between the emissary foramina and the diploic veins of the skull, which is probably of importance in the spread of infection from the exterior of the skull.

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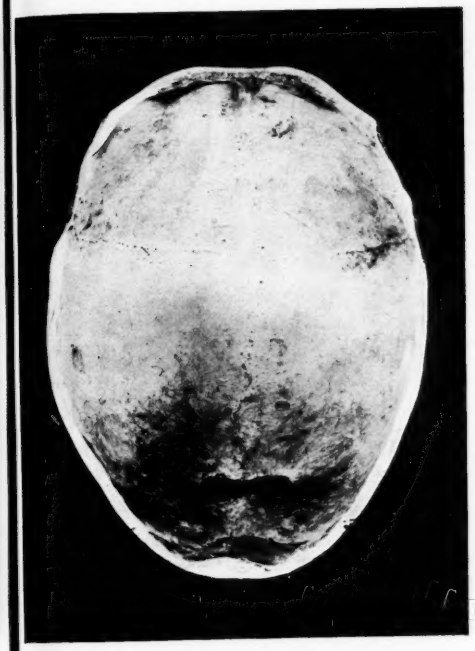

Fig. 1

Fig. 2

Fig. 3

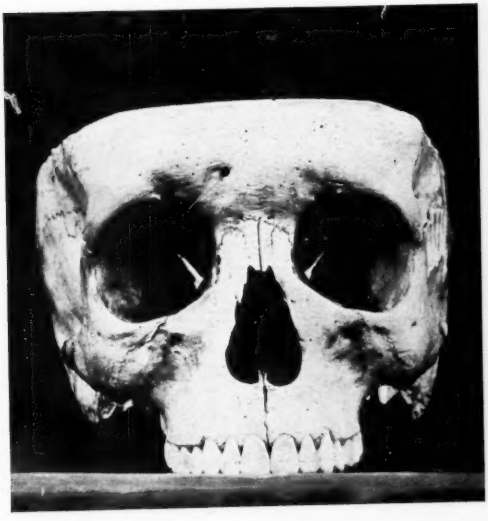

Fig. 4

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EXPLANATION OF PLATE I

Fig. 1. Photograph of skull vault showing enlarged parietal foramina (same specimen as fig. 2).
Fig. 2. Radiogram showing enlarged parietal foramina (same specimen as fig. 1).
Fig. 3. Photograph of skull showing unilateral large parietal foramen.
Fig. 4. Photograph of skull showing emissary canal in the frontal bone.

CRANIOMETRIC MEMOIRS

No. III. THE SUPERIOR GNATHIC TRIANGLE. A NEW CRANIAL TRIANGLE. ITS SIGNIFICANCE IN MODERN AND FOSSIL MAN, THE ANTHROPOIDS AND LOWER MAMMALS

By JOHN CAMERON, M.D., D.Sc.

Professor of Anatomy, Dalhousie University, Halifax, N.S.

The alveolar or gnathic index devised by Flower (9) has proved to be one of the most valuable of the cranial indices. It has, however, been by no means free from criticism. For instance, Thomson (12) has very rightly pointed out that "it takes no account of the proportion of the third or facial side of the gnathic triangle." The latter triangle, it may be mentioned, has its salients at the nasion, the basion and the alveolar point. It formed the subject of a recent study by the present writer (4), and as a result he found that the completed triangle did not sufficiently demonstrate some of the conditions that are associated with maxillary projection or prognathism. This fact was brought very vividly to the writer's mind, when he was engaged in the examination of the Eskimo crania of the Canadian Arctic Expedition, 1913–18 (1). He found that prognathism did not exist at all in the male crania but, on the other hand, it was exhibited by nine out of the total of fifteen female crania that were available for the study of this particular point. He was interested to notice, however, that in these nine female crania the prognathic condition affected only those portions of the maxillae below the level of the nasal apertures. For this reason he coined a new word to describe this form of prognathism, and termed it the subnasal variety. The amount of subnasal projection in some of these female Eskimo crania was most marked. For example, one skull possessed an alveolar index as high as 107·4, which was of course to be regarded as extreme, thus indicating a high degree of subnasal prognathism. The problem that the author had to set himself, therefore, was to ascertain to what extent prognathism was subnasal and to what extent it was nasal in the various types representative both of Man and of lower Mammals that might be available to him. He questioned very much to what extent the term "nasal" might be felicitous or even appropriate, as a contrast to the term "subnasal." As the upper portions of the maxillae do take a very vital part in the formation of the nasal fossae, the above terms both sounded feasible. However, that seemed to him not enough. His next course, therefore, was to devise two triangles, which he termed the superior and inferior gnathic triangles. These are represented in fig. 1. This meant also the devising of a new

craniometric point which would be the means of demarcating these two triangles anteriorly. After much deliberation, he decided to select a point which he has termed the subnasion. He has described this in a recent paper (7), and has defined it as "the point where a line connecting Hrdlicka's two subnasal points crosses the median plane of the skull." As fig. 1 shows, the three salients of the superior gnathic triangle are at the nasion, basion and subnasion, while those for the inferior gnathic triangle are at the basion, subnasion and alveolar point.

This memoir is founded mainly upon research work that was conducted in the Hamann Museum, Western Reserve University. The writer, therefore, desires to pay a tribute of thanks to Prof. T. Wingate Todd for the unlimited facilities afforded to him during the progress of the research. The material representing modern Man consisted of 60 male White, 60 female White, 60 male Negro and 60 female Negro crania. The Museum also contained reconstructions of the Rhodesian skull, the La Chapelle skull, and the Combe Capelle skull, representing fossil Man. He had also the use of crania of the four higher anthropoids, while *Pithecus* was utilised to represent the lower anthropoids. The lemur group was represented by *Lemur catta*, and by *Tarsius*, which, by the way, provided a most interesting study. The skull of a dog proved a useful representative of the Carnivora. The writer also expresses his gratitude to Dr Ales Hrdlicka for the privilege of studying 33 male Greenland Eskimo crania, 33 male Mongol crania and 5 native Australian crania (unsexed) in the U.S. National Museum. He wishes to thank Dr J. M. Ingersoll for the use of gibbon and orang skulls. The writer wishes to pay his acknowledgments to his wife for valuable help in measuring vast numbers of crania in the heat of a continental summer, and in checking long lists of measurements and calculations.

It is essential to mention at this point the procedure that was adopted by the author to estimate the angles of the superior gnathic triangle. The nasion-basion, basion-subnasion and nasion-subnasion dimensions were measured on each skull, and the triangle was plotted out on a sheet of paper from these measurements by means of a pair of compasses. It was found important to make very fine lines for each side of the triangle with a sharp pencil, so as not to vitiate the size of each angle. The three angles were then estimated by means of a celluloid goniometer. The process was a long and tedious one, requiring much care and patience.

This investigation became naturally divided into two parts, namely, a study of the three sides of the superior gnathic triangle, and a study of its three constituent angles. Of the three sides, the nasion-basion length is of course a long-established cranial dimension. The writer made a comparative study of it in various racial types of modern Man a few years ago (3), so that it will be unnecessary to dilate further on that topic at this juncture. The other two sides of the triangle, namely the nasion-subnasion and the basion-subnasion dimensions, have of course never been previously described. They are therefore

to form the subject of a separate communication, which is being published elsewhere(5). It is important to mention that the writer has also made a study of the relative proportions of the three sides of this triangle in Man and in lower Mammals. In this way three new cranial indices have been produced. These have been found to possess a considerable degree of significance, and

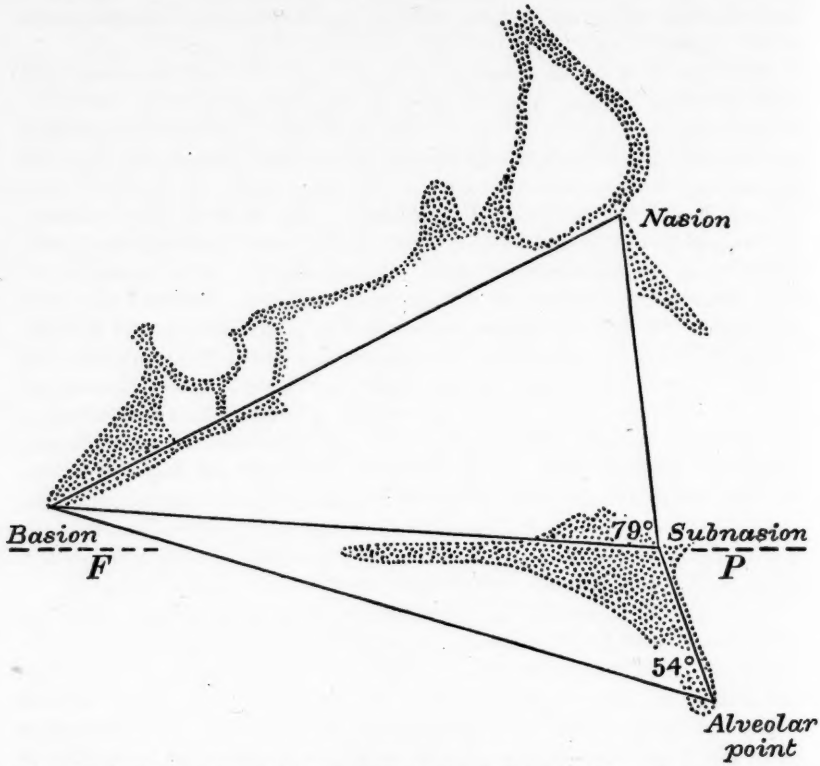

Fig. 1. Part of the mesial section of a male Melanesian skull, to show the gnathic triangles that have been devised by the author. The superior gnathic triangle has its salients at the nasion, basion and subnasion, those for the inferior gnathic triangle being at the basion, subnasion and alveolar point. The short dotted lines marked *F* and *P* represent a plane parallel to the Frankfort plane.

they will also be dealt with in a separate communication(6). The theme of this present paper, therefore, will be a study of the human and comparative anatomy of the three constituent angles of the superior gnathic triangle. Their salients are situated at the nasion, basion and subnasion, and they will, for the sake of brevity, be referred to in this paper as the S.-N.-B., N.-B.-S. and N.-S.-B. angles respectively of the superior gnathic triangle (fig. 1).

I. THE N.-S.-B. ANGLE OF THE SUPERIOR GNATHIC TRIANGLE

The salient of the N.-S.-B. angle of the superior gnathic triangle is situated at the subnasion (fig. 1). It exhibited wide ranges of variation in both the White and the Negro crania of the Hamann Museum. The standard deviations and the coefficients of variability were moderately large.

Table I. *The N.-S.-B. angle of the superior gnathic triangle exhibited the usual wide ranges of variation in the Hamann Museum White and Negro crania*

	Maximum	Minimum	Range of variation
Hamann Museum male White	97°	76°	21°
Hamann Museum female White	96°	75°	21°
Hamann Museum male Negro	92°	70·6°	21·4°
Hamann Museum female Negro	90·6°	72°	18·6°

Table II. *The standard deviations and coefficients of variability of the N.-S.-B. angle of the superior gnathic triangle in the Hamann Museum White and Negro crania*

	Standard deviations	Coefficients of variability
Hamann Museum male White	3·91 ± 0·3197	4·76 ± 0·3893
Hamann Museum male Negro	3·95 ± 0·32307	4·96 ± 0·4056
Hamann Museum female White	4·84 ± 0·3958	5·86 ± 0·4792
Hamann Museum female Negro	3·32 ± 0·2715	4·20 ± 0·3435

The average size of the N.-S.-B. angle of the superior gnathic triangle

The average size of this angle in the Hamann Museum male White crania proved to be 81·8°. In the male Negroes it was found to be definitely less, namely 79·6°. Further investigation showed that this racial difference was likewise exhibited by the female crania. Thus the average size of the N.-S.-B. angle in the female White crania was 82·4°, as opposed to 79·1° for the female Negroes. It was therefore evident that this angle tended to approximate to a right angle in the orthognathic skull of the White races, and to become smaller in the more prognathic Negro. This indicated, of course, that the subnasion was projected forwards to a greater degree in the prognathic than in the orthognathic type of skull. In addition, one obtained definite information to prove that the superior gnathic triangle exhibited only a slight degree of involvement in the prognathism of the Negro and other prognathic races (see fig. 1).

There could thus be no dubiety regarding the fact that the N.-S.-B. angle of the superior gnathic triangle tended to exhibit its maximum dimensions in the orthognathic type of skull, and also that it became smaller with increasing degrees of prognathism. The next step in the investigation therefore was to put this to the test in the other racial types of modern Man that were available. For example, in the Greenland Eskimo male skull this angle registered an average dimension of 80·3°. This meant that these crania were on the average slightly less orthognathic than the Hamann Museum male White crania, and in this respect occupied a position intermediate between

the Hamann Museum White and Negro crania. In other words they fell into the mesognathic group of Flower (9).

The male Mongol crania, it should be mentioned, all came from Urga in Mongolia. Their average N.-S.-B. angle proved to be as much as 81·6°, that is to say, practically the same as that for the male White crania. At this point the writer cannot refrain from mentioning the fact that he was very favourably impressed by the fine appearance presented by these Mongol crania. As Hrdlicka (10) has shown, they displayed the high average cranial capacity of 1573 c.c., and, judging from the high average dimensions of their N.-S.-B. angles just given, they were remarkably orthognathic in appearance. In fact, they were the finest looking crania, taken as a group, that the author has ever had the privilege of measuring.

The other extreme was manifested by the native Australian crania, for in them the N.-S.-B. angle recorded the low average of 78·6°. Indeed this represented the lowest ebb for all the racial types representing modern Man that were available for study. Two low grade male Melanesian crania (2) recorded angles of 79·3° and 77°, the average for which would accord with that for the native Australian. At some future time the writer hopes to be in a position to study the dimensions of this angle in an interesting ethnic type like the native Tasmanian.

The study of the N.-S.-B. angle in the specimens representative of fossil Man provided some interesting data, though these will have to be taken as approximate, seeing that the various measurements were taken from casts of the original crania. The lowest dimension was recorded by the La Chapelle skull, which yielded an angle of only 71°, that is to say, far below the averages even for the black races of modern Man. This low result indicated that the subnasion point was projected very far forwards in this specimen. Indeed this was so, for its basion-subnasion dimension was as much as 126·5 mm., an extreme figure when compared with an average of only 91·8 mm. for this cranial length in the Hamann Museum male White. It was thus clear that the superior gnathic triangle contributed to the prognathism of the La Chapelle skull in a considerable degree. The dimension yielded by this angle in the Rhodesian cast was much higher, namely 77·6°. This, however, was still below the average for the native Australian. Even so, it indicated that the superior gnathic triangle of the Rhodesian skull was not nearly so prognathic as that of the La Chapelle skull. The Combe Capelle cast made a better showing, for it recorded a N.-S.-B. angle of 79·3°. That is to say, it approximated much more closely to the average for the European type of skull than did the La Chapelle specimen. It will be noted that the results of the study of this cranial angle in modern and fossil Man have been recorded in Table III. The writer calculated at the same time the gnathic indices for all the cranial groups that were examined. He has inserted these in the same table for the purpose of demonstrating the fact that the N.-S.-B. angle diminishes, while the gnathic index increases, with progressive degrees of prognathism. It should

be clearly understood, however, that the N.-S.-B. angle is an index of prognathism affecting only the superior gnathic triangle, whereas the gnathic index is an index of prognathism involving the whole gnathic triangle. The gnathic indices that are given for fossil Man in Table III will have to be accepted as approximate, on account of the fact that these had to be calculated from measurements made upon casts. The index for the Rhodesian skull was taken from Pycraft's memoir (11). The original crania were of course quite inaccessible.

Table III. *The N.-S.-B. angle of the superior gnathic triangle in modern and fossil Man. Note that this angle diminishes, while the gnathic index increases, with progressive degrees of prognathism*

	N.-S.-B. angle	Gnathic index
Male White (Hamann Museum)	81·8°	92·9
Male Mongol (U.S. National Museum) ...	81·6°	95·4
Male Eskimo (U.S. National Museum) ...	80·3°	97·6
Combe Capelle skull (approx.)	79·3°	96·8
Male Negro (Hamann Museum)	79·6°	100·8
Australian native (U.S. National Museum)	78·6°	100·6
Rhodesian skull (approx.)	77·6°	105·0
La Chapelle skull (approx.)	71·5°	105·9

Comparative anatomy of the N.-S.-B. angle of the superior gnathic triangle

Our investigations on this angle in modern and fossil Man have informed us that it attained its maximum dimensions in the orthognathic type of skull, and became gradually smaller with increasing degrees of prognathism. A reduction in the size of the angle thus meant that the subnasion point was being displaced in a forward direction (see fig. 1). In addition to these findings, it was obvious that the dimensions of the angle provided us with an index of the degree to which the superior gnathic triangle was involved in protrusion of the maxillae. In other words, the smaller the angle, the greater was the amount of involvement of the triangle in prognathism. As a natural outcome to these observations, one would expect the N.-S.-B. angle to continue to exhibit this progressive diminution in size as one descended the mammalian phylum. As a matter of fact, this diminution was found to be quite pronounced. For example, the skull of a chimpanzee (B. 240 of the Hamann Museum) possessed a N.-S.-B. angle of only 57°. Of the three highest anthropoids, this was the one that showed the nearest approximation to the Hominidae, so far as the size of this angle was concerned. There was thus a very wide evolutionary gap in this portion of the mammalian scale, as shown in Table IV. Of the other two highest anthropoids, a gorilla skull (B. 170 of the Hamann Museum) yielded an angle of 54·3°, and that of an orang (B. 551 of the Hamann Museum) an angle of 54·6°. It may therefore be noted that the orang skull made a better showing than the gorilla skull, though the difference was merely fractional. The result yielded by a gibbon skull (B. 549 of the Hamann Museum) was rather surprising, for it furnished a N.-S.-B. angle of 59·6°, that is to say, larger even than the angle furnished by the chimpanzee skull. It was thus

evident that this angle displayed in the anthropoids the usual ranges of variation, just as was found in Man. Therefore in order to strike an average, large numbers of crania would have to be available. Unfortunately only one mesially sectioned skull was available to represent each genus for the particular purpose of this investigation, the results of which, for the lower mammalia at any rate, had better be regarded as a preliminary communication.

The skull of *Pithecus* (B. 416 of the Hamann Museum) was selected to represent the lower anthropoids. It yielded a N.-S.-B. angle of 57°, which, it may be noted, was exactly the same as that recorded by the chimpanzee skull. On coming to the lemuroidea, it was ascertained that the skull of *Lemur catta* (B. 197 of the Hamann Museum) furnished an angle of only 38·6°, as one would expect in a mammalian type below the level of the anthropoids. It was all the more surprising to note that a skull of *Tarsius* (B. 135 of the Hamann Museum) exhibited a N.-S.-B. angle as high as 57·6°, which was almost exactly half as much again as that obtained from the skull of *Lemur catta*. Indeed it was fractionally greater even than that shown by the chimpanzee. It is well known that a great deal of interest has centred round *Tarsius* from the evolutionary standpoint. It was therefore all the more satisfactory to be able to place on record one more item of knowledge regarding this most important member of the lemuroidea. The author has already directed attention to the remarkably advanced evolutionary phase exhibited by the cranio-facial axis in this genus (8). Certainly the dimensions of its N.-S.-B. angle placed this skull of *Tarsius* in a very favourable position in the evolutionary scale. The skull of this dainty little animal is of course extremely small, so that the author was compelled to adopt a special procedure, in order to be enabled to study its superior gnathic triangle. Prof. Wingate Todd very kindly took a photograph of a mesial section of the skull, and from this an enlargement was prepared, magnified five times. The triangle was plotted out on paper from measurements of its three sides made on this enlargement. The three angles were then estimated by means of a celluloid goniometer, as explained in the introduction to this paper.

The only mesially sectioned skull that was available to represent the lower mammalia in this investigation was that of a dog (B. 128 of the Hamann Museum). At this point the author feels it his duty to record the fact that Prof. Wingate Todd made a special concession in consenting to the sectioning of this skull, which was very skilfully done by Mr Leonhart. The N.-S.-B. angle in this specimen recorded only 30°, which represented the minimum for all the mammalian types that were available for study. On comparing this dimension with that found in the higher Hominidae, it may be noted that the size of the angle had become reduced by nearly two-thirds, certainly a very spectacular reduction. It meant of course that the subnasion point had become projected forwards to a marked degree in this skull. In other words, its superior gnathic triangle had become profoundly affected by prognathism.

Table IV. *The N.-S.-B. angle of the superior gnathic triangle exhibits a progressive diminution in size, as one descends the mammalian phylum. Note the vast evolutionary gap between the Hominidae and the highest anthropoids. Note also the relatively large size of the angle shown by* Tarsius

		Evolutionary gap	
Hamann Museum male White	81·8°	Chimpanzee	57°
Hamann Museum male Negro	79·6°	Gorilla ...	54·3°
Australian native (U.S. National Museum)	78·6°	Orang ...	54·6°
Rhodesian skull (cast)	77·6°	Gibbon ...	59·6°
La Chapelle skull (cast)	71·5°	*Pithecus* ...	57°
		Lemur ...	38·6°
		Tarsius ...	57·6°
		Dog ...	30°

II. THE S.-N.-B. ANGLE OF THE SUPERIOR GNATHIC TRIANGLE

The salient of the S.-N.-B. angle of the superior gnathic triangle is situated at the nasion (fig. 1). It exhibited fairly extensive ranges of variation in the Hamann Museum White and Negro crania. The standard deviations and the coefficients of variability were moderately large.

Table V. *The ranges of variation of the S.-N.-B. angle of the superior gnathic triangle in the Hamann Museum White and Negro crania*

	Maximum	Minimum	Range of variation
Hamann Museum male White	75°	53·6°	21·4°
Hamann Museum female White	77°	57·5°	19·5°
Hamann Museum male Negro	74°	58°	16°
Hamann Museum female Negro	78°	59°	19°

Table VI. *The standard deviations and coefficients of variability of the S.-N.-B. angle of the superior gnathic triangle in the Hamann Museum White and Negro crania*

	Standard deviation	Coefficient of variability
Hamann Museum male White	4·17 ± 0·34106	6·36 ± 0·5201
Hamann Museum female White	4·47 ± 0·3656	6·82 ± 0·5578
Hamann Museum male Negro	4·59 ± 0·3754	6·70 ± 0·5479
Hamann Museum female Negro	4·21 ± 0·3443	6·01 ± 0·4915

The average size of the S.-N.-B. angle of the superior gnathic triangle

The average size of this angle in the Hamann Museum male White crania was estimated to be 65·7°. In the male Negro crania, on the other hand, it was found to be definitely greater, namely 68·6°. This racial difference was to be expected, for if the angle be studied in fig. 1, it will be noted that it would tend to show a gradual increase, with progressive degrees of prognathism. This racial difference was displayed also by the Hamann Museum female crania. For instance, the average size of the S.-N.-B. angle in the female White crania proved to be 65·7°, that is to say, exactly the same as that for the male White crania. The female Negro crania provided a striking contrast

to this result, by furnishing an average size of angle amounting to 69·8°. There could therefore be no question regarding the fact that the S.-N.-B. angle became definitely involved in prognathism affecting the superior gnathic triangle.

The next ethnic type that was studied was the Greenland Eskimo. In this cranial group the average size of the S.-N.-B. angle proved to be 68·3°. This result signified that the superior gnathic triangle in these crania was on the average slightly less prognathic than the Hamann Museum Negro crania and less orthognathic than the White crania.

The average size of the S.-N.-B. angle in the male Mongol crania was estimated to be 64·1°, that is to say, lower than the average for the White crania. This indicated of course that the superior gnathic triangle in this racial group was on the average more orthognathic even than in the White crania. Indeed this fact was recently confirmed by the author (6) as the result of an investigation on the indices of this triangle. As a contrast to this, the writer found that the average size of the S.-N.-B. angle in the native Australian crania was as much as 72·6°. This was the highest figure recorded for all the racial types representative of modern Man that were available for this research. It indicated of course that the superior gnathic triangle in that ethnic group was markedly involved in prognathism. It should be noted that a male Melanesian skull, representing another interesting racial type from the Australasian area, yielded a S.-N.-B. angle of 71·3°, which approximated to the average for the native Australian crania.

The study of the S.-N.-B. angle in fossil Man, though it had to be conducted on casts, provided some interesting and indeed startling results. For instance, the La Chapelle skull yielded an angle measuring as much as 79·8°. An inspection of Table V will show that this extreme dimension was beyond the maximum range for modern Man. It therefore indicated that prognathism had involved the superior gnathic triangle of the La Chapelle skull to a marked degree. The cast of the Rhodesian skull presented a S.-N.-B. angle more than ten degrees less, the actual figure being 69°. As Table VII shows, this closely accorded with the average for the Hamann Museum Negro crania. The angle for the Combe Capelle skull was slightly less, namely 68·6°.

The results of this study of the S.-N.-B. angle of the superior gnathic triangle have been recorded in Table VII. The writer calculated at the same time the gnathic indices for all the crania that were examined. These have therefore been inserted in the same table for the purpose of demonstrating that the gnathic index and the dimensions of the S.-N.-B. angle follow one another more or less consistently. That is to say, both increase with progressive degrees of prognathism. It should be clearly noted, however, that the S.-N.-B. angle is an index of prognathism affecting only the superior gnathic triangle, whereas the gnathic index is an index of prognathism involving the whole gnathic triangle.

Table VII. *The gnathic index and the dimensions of the S.-N.-B. angle follow one another more or less consistently. That is to say, both increase with progressive degrees of prognathism*

	S.-N.-B. angle	Gnathic index
Male White (Hamann Museum)	65·7°	92·9
Male Mongol (U.S. National Museum) ...	64·1°	95·4
Male Eskimo (U.S. National Museum) ...	68·3°	97·6
Combe Capelle skull (approx.)	68·6°	96·8
Male Negro (Hamann Museum)	68·6°	100·8
Australian native (U.S. National Museum)	72·6°	100·6
Rhodesian skull (approx.)	69°	105
La Chapelle skull (approx.)	79·3°	105·9

Comparative anatomy of the S.-N.-B. angle of the superior gnathic triangle

The results obtained from a study of this angle in modern and fossil Man were decisive. That is to say, we obtained information to the effect that it was an index of the degree of prognathism involving the superior gnathic triangle. Thus it was ascertained that the angle exhibited a characteristic increase, dependent upon the degree of projection of the maxillae. Therefore it was to be concluded that this increase in the dimensions of the S.-N.-B. angle would be exhibited in full measure by the markedly prognathic crania of lower Mammals. This question was studied first of all in the three highest anthropoids. As a result, it was ascertained that the skull which approximated most closely to the Hominidae, so far as this angle was concerned, was that of a gorilla (B. 170 of the Hamann Museum). This specimen yielded an angle of 88·5°, which represented an increase of 23°, when compared with the average size of the angle in the White crania. It was thus manifest that a very extensive evolutionary gap existed between the Hominidae and the Simiidae, so far as the dimensions of this angle were concerned. The angle furnished by the skull of a chimpanzee (B. 240 of the Hamann Museum) and that of an orang (B. 551 of the Hamann Museum) was exactly similar, namely 94°. This also happened to be the dimensions of the angle shown by the skull of a gibbon (B. 549 of the Hamann Museum). A skull of *Pithecus* (B. 416 of the Hamann Museum), which was chosen to represent the lower anthropoids, provided an angle which, as was to be expected, proved to be fractionally larger, namely 94·5°.

The lemuroidea were represented in this investigation by the crania of two genera, which provided a most astonishing contrast. A skull of *Lemur catta* (B. 197 of the Hamann Museum), as was to be anticipated, exhibited an angle much greater than those shown by the anthropoidea, namely 118·6°. The author was therefore greatly surprised to find that the S.-N.-B. angle furnished by a skull of *Tarsius* (B. 135 of the Hamann Museum) was only 92·3°, that is to say, less than that displayed by any of the highest anthropoids, with the exception of the gorilla skull (Table VIII). It was thus evident that the skull of *Tarsius*, so far as this cranial angle was concerned, was placed in a very favourable position in the evolutionary scale.

The lower mammalia were represented by the skull of a dog (B. 128 of the

Hamann Museum). As was to be expected, the S.-N.-B. angle displayed a further increase in this skull, when compared with that found in *Lemur catta*, the actual figure being 124°. This represented a dimension nearly twice as great as the average for the higher Hominidae.

Table VIII. *The S.-N.-B. angle of the superior gnathic triangle exhibits a progressive increase in size, as one descends the mammalian series. Note the vast evolutionary gap between the Hominidae and the highest anthropoids. Note also the relatively small size of the angle shown by* Tarsius

		Evolutionary gap	
Hamann Museum male White	65·7°	Gorilla ...	88·5°
Hamann Museum male Negro	68·6°	Chimpanzee	94°
Australian native (U.S. National Museum)	72·6°	Orang ...	94°
Rhodesian skull (approx.)	69°	Gibbon ...	94°
La Chapelle skull (approx.)	79·3°	*Pithecus* ...	94·5°
		Lemur ...	118·6°
		Tarsius ...	92·3°
		Dog ...	124°

III. THE N.-B.-S. ANGLE OF THE SUPERIOR GNATHIC TRIANGLE

The salient of the N.-B.-S. angle is situated at the basion. It is by far the smallest of the three constituent angles of the superior gnathic triangle. It exhibited the usual ranges of variation in the Hamann Museum White and Negro crania. The standard deviations and coefficients of variability were moderately small.

Table IX. *The ranges of variation of the N.-B.-S. angle of the superior gnathic triangle in the Hamann Museum White and Negro crania*

	Maximum	Minimum	Range of variation
Hamann Museum male White	37°	29°	8°
Hamann Museum female White	37°	27·5°	9·5°
Hamann Museum male Negro	36·5°	26·5°	10°
Hamann Museum female Negro	34·6°	27·3°	7·3°

Table X. *The standard deviations and coefficients of variability of the N.-B.-S. angle of the superior gnathic triangle in the Hamann Museum White and Negro crania*

	Standard deviations	Coefficients of variability
Hamann Museum male White	1·96 ±0·1603	6·03 ±0·4931
Hamann Museum female White	2·49 ±0·2036	7·77 ±0·6355
Hamann Museum male Negro	2·48 ±0·2028	7·87 ±0·6436
Hamann Museum female Negro	1·94 ±0·1586	6·25 ±0·5111

The average size of the N.-B.-S. angle of the superior gnathic triangle

The average dimensions of this angle in the case of the Hamann Museum male White crania proved to be 32·4°. As a contrast to this, it was ascertained that the average for the male Negro crania was slightly less, the actual figure being 31·5°. The racial difference was thus not so marked as in the case of the

other two angles of the triangle. It had to be recollected, however, that the size of the N.-B.-S. angle was very much less than that of the other two. Therefore if the above racial difference were to be reduced to a percentage basis, it would really be found to be quite considerable.

The above results were confirmed by an examination of the female crania. For instance, the average size of the N.-B.-S. angle in the female White crania was 31·9°, whereas in the female Negroes it was again less, namely 30·9°. The information yielded so far indicated that this angle tended to become reduced in size in the more prognathic types of crania.

The average size of the N.-B.-S. angle in the Greenland Eskimo male crania was 31·3°, that is to say, practically the same as that for the Hamann Museum male Negro. The male Mongol crania, on the other hand, furnished an average size of angle amounting to 34·3°. This proved to be the highest average for all the racial types that were examined in this research. As a contrast to this high figure, the native Australian crania provided the lowest racial average for all the representative types of modern Man that were available for this investigation, the actual figure being 28·6°. This result therefore confirmed our previous observation that the N.-B.-S. angle tended to become reduced in size with progressive degrees of prognathism.

The results obtained from a study of the specimens representing fossil Man were rather diverse in character. The lowest dimension was that recorded by the La Chapelle skull, namely 29°. This result was, of course, below the average for modern Man, and, indeed, confirmed the observations made on the other two constituent angles of the superior gnathic triangle. That is to say, it indicated that this triangle was affected by prognathism in a very marked degree in the La Chapelle skull. As was to be expected, the Combe Capelle skull exhibited a N.-B.-S. angle of slightly larger dimensions, namely 31°, though this was below the average found in the Hamann Museum White crania. The Rhodesian skull provided an angle as large as 32·6°, which was greater than one would have expected in such a low grade skull.

Table XI. *The N.-B.-S. angle of the superior gnathic triangle attains its maximum dimensions in the higher Hominidae, and becomes reduced in size in the lower races of modern Man*

Male White (Hamann Museum)	32·4°
Male Mongol (U.S. National Museum) ...	34·3°
Male Eskimo (U.S. National Museum) ...	31·3°
Male Negro (Hamann Museum)	31·5°
Australian native (U.S. National Museum)	28·6°

Comparative anatomy of the N.-B.-S. angle of the superior gnathic triangle

The results yielded so far from a study of this angle have indicated that it reaches its maximum dimensions in the higher Hominidae, and becomes reduced in size in the lower races of mankind. Upon pursuing this investigation into the higher anthropoids, it was ascertained that there was no definite

evolutionary gap between these and the Hominidae in the case of this angle. This gap, it may be recollected, was quite extensive in the case of the other two angles of the triangle. For example, the skull of a chimpanzee (B. 240 of the Hamann Museum) furnished a N.-B.-S. angle of 29·3°, which was within the range of variability even for the higher Hominidae (Table IX). The skull of a gorilla (B. 170 of the Hamann Museum) yielded a surprisingly large angle, namely 37°. This fact suggested that the N.-B.-S. angle displayed wide ranges of variation in the anthropoids just as in Man. An orang skull (B. 551 of the Hamann Museum) provided an angle larger than that exhibited by the chimpanzee, namely 31·6°. It was found to be definitely smaller, namely 26·3°, in the skull of a gibbon (B. 549 of the Hamann Museum). A macaque monkey (B. 416 of the Hamann Museum) displayed an angle of 29·3°, while, as was to be expected, it was decidedly smaller, namely 23·3°, in a skull of *Lemur catta* (B. 197 of the Hamann Museum). One was therefore all the more surprised to find that a skull of *Tarsius* (B. 135 of the Hamann Museum) presented a N.-B.-S. angle as large as 30°. That is to say, it was larger in this member of the lemuroidea than in the chimpanzee skull. One therefore cannot but be impressed by the favourable showing of all three angles of the superior gnathic triangle in *Tarsius*. The skull of a dog (B. 128 of the Hamann Museum) possessed a N.-B.-S. angle of 26·3°. There could thus be no doubt regarding the fact that this angle tended to become reduced in dimensions in lower Mammals, although the amount of reduction in the higher anthropoids was not very decisive.

General discussion of all three angles of the superior gnathic triangle

It may be noted in the first place that the three angles of the superior gnathic triangle were all definitely affected by prognathism involving this cranial triangle. It may be further observed that the N.-S.-B. and the N.-B.-S. angles diminished, while the S.-N.-B. angle increased in size, as one descended the mammalian phylum. That is to say, all three angles became profoundly affected by the prognathism of lower Mammals. The most spectacular changes were exhibited by the N.-S.-B. angle, which was found to become reduced by nearly two-thirds in lower Mammals (e.g. the dog), when compared with its average dimensions in the higher Hominidae. The S.-N.-B. angle, on the other hand, became so enormously increased in size, as one descended the mammalian series, that in some lower Mammals (e.g. the dog) it had become enlarged to twice the size, when contrasted with its average dimensions in the White races. The N.-B.-S. angle, being the smallest constituent angle of the superior gnathic triangle, did not display such striking changes in its dimensions, as one descended the mammalian scale. It did, however, become definitely reduced in size in lower Mammals.

The N.-S.-B. and the S.-N.-B. angles displayed very wide evolutionary gaps between the Hominidae and the higher anthropoids (Table XI). In the case of the N.-B.-S. angle, however, there was no such gap. All three angles

displayed dimensions in the anthropoid group that were remarkably close. Between them and the lemuroidea, as represented for instance by *Lemur catta*, another definite evolutionary gap could be detected in the case of each angle. This fact brought into prominence the remarkable position occupied by *Tarsius* in the mammalian scale. All three angles in this member of the lemur group exhibited dimensions which compared favourably even with those displayed by the highest anthropoids. This fact was of great importance in relation to the interesting discussions that have taken place regarding the position occupied by *Tarsius* in the evolutionary scale. Of course it should be noted that only one mesially sectioned skull was available to represent each genus of the anthropoidea and the lemuroidea, so that one has to recognise the influence of the range of variation. However, the difference between the dimensions of all three angles in *Tarsius* and those displayed by *Lemur catta* was so outstanding that it would be hard to convince oneself that they could be explained by the ranges of variation.

Table XII. *The N.-S.-B. and the N.-B.-S. angles of the superior gnathic triangle diminish, and the S.-N.-B. angle increases, as one descends the mammalian scale. Note the evolutionary gaps and also the remarkable position occupied by the* Tarsius *skull in the evolutionary scale*

	N.-S.-B. angle	S.-N.-B. angle	N.-B.-S. angle
Male White (Hamann Museum)	81·8°	65·7°	32·4°
Male Negro (Hamann Museum)	79·6°	68·6°	31·5°
Australian native (U.S. National Museum)	78·6°	72·6°	28·6°
	Evolutionary gaps		No gap
Tarsius	57·6°	92·3°	30°
Chimpanzee	57°	94°	29·3°
Gorilla	54·3°	88·5°	37°
Orang	54·6°	94°	31·6°
Gibbon	59·6°	94°	26·3°
Pithecus	57°	94·5°	29·3°
Lemur	38·6°	118·6°	23·3°
Dog	30°	124°	26°

CONCLUSIONS

1. The superior gnathic triangle is a new cranial triangle recently devised by the author.

2. Its three constituent angles are described for the first time in this paper.

3. The salients of the superior gnathic triangle are at the nasion, basion and subnasion, the last being a new craniometric point devised by the author. The three angles are therefore the nasion-subnasion-basion (N.-S.-B.), the subnasion-nasion-basion (S.-N.-B.) and the nasion-basion-subnasion (N.-B.-S.).

4. All three angles were definitely affected by prognathism involving the superior gnathic triangle. They all exhibited alterations in their dimensions in the Black races, when compared with the White races.

5. The dimensions of all three angles became profoundly affected by the prognathism of lower Mammals. For example, the N.-S.-B. and the N.-B.-S. angles diminished, while the S.-N.-B. angle increased in size, as one descended the mammalian phylum.

6. This research brought into prominence the remarkable position occupied by *Tarsius* in the evolutionary scale. All three angles in this member of the lemuroidea exhibited dimensions which compared favourably even with those displayed by the highest anthropoids. This fact would of course have to be confirmed by the study of large numbers of mesially sectioned crania representative of the anthropoidea and the lemuroidea.

7. The superior gnathic triangle of the La Chapelle skull displayed a much more marked degree of prognathism than that shown by the Rhodesian and Combe Capelle crania. These observations were all made on casts of the original skulls.

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A DEVELOPMENTAL ABNORMALITY OF A LIZARD'S HEART

By RUPERT A. WILLIS, M.D. (Melbourne)

Medical Superintendent, Austin Hospital for Chronic Diseases, Heidelberg, Victoria, Australia

While engaged in a series of experiments involving the dissection of a number of blue-tongued lizards (*Tiliqua Scincoides*), the writer observed in one specimen a remarkable developmental abnormality of the heart, which is worthy of record.

The animal was dissected immediately after death by chloroformisation and while the heart was still beating normally[1]. Attention was attracted to the cardiac abnormality by observing, with the pericardial sac still unopened, that the systolic sequence appeared to be reversed, apical systole occurring before basal systole in each cardiac cycle. On opening the pericardium, this was found to be the case; the pale thick-walled ventricle lying at the base of the organ, while the large dark thin-walled auricle lay distally in the apical position. The viscera were fixed *in situ* by immersion of the whole body in 10 per cent. formalin; and the heart and other organs thereafter carefully dissected.

The normal heart of *Tiliqua* is typically lacertilian in structure. There are three principal chambers, right and left auricles situated basally, and a single apical ventricle. A small sinus venosus receives the systemic venous blood from the two pre-caval and the single post-caval veins. The sinus opens into the right auricle *via* a slit-like aperture guarded by a pair of valve cusps. The pulmonary vein opens directly into the left auricle. The two auricular chambers are separated by a complete septum. Each auricle opens into the ventricle through a narrow orifice guarded by a large valve cusp. The two auriculo-ventricular apertures are situated close together, one on each side of the inter-auricular septum, to the lower border of which the valve cusps are attached. The ventricle is complex and highly trabeculated. The conus arteriosus arising from it is compound, consisting of the pulmonary artery, the left systemic artery, and the right systemo-carotid artery, all bound together within a common sheath. For further details and valuable diagrams of the anatomy of the normal heart of *Tiliqua Scincoides*, the reader is referred to the article by Subba Rau (1924) published in this *Journal*.

[1] The heart continues to beat for many hours. The writer has observed regular auricular systoles for as many as 30 hours after death.

DESCRIPTION OF THE DEFORMED HEART

Figs. 1 and 2 represent the external appearance of the organ. These figures are largely self-explanatory, but attention may be directed to several points. The sinus venosus, formed normally by the confluence of the three caval veins, was decidedly larger than normal, forming a prominent bulbous chamber posterior to the base of the right auricular region. The gubernaculum cordis, a band of pericardial tissue which normally anchors the apex of the ventricle to the left posterior wall of the pericardial sac, was absent. The auricular or apical half of the organ lay entirely free in the pericardial cavity. The basal ventricle was very firmly attached posteriorly to the caudal part of the trachea. The pericardial reflexions at the margins of this area evidently represented the displaced gubernacular attachment.

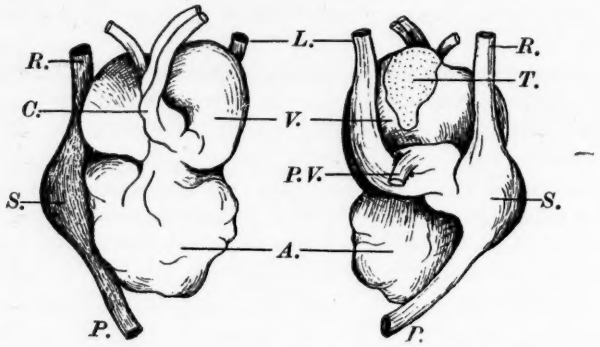

Fig. 1. Anterior view of heart. Fig. 2. Posterior view of heart.

A. auricle; *V.* ventricle; *S.* sinus venosus; *R.* right pre-caval vein; *L.* left pre-caval vein; *P.* post-caval vein; *P.V.* pulmonary vein; *C.* conus arteriosus; *T.* area of ventricle in contact with trachea. (Twice normal size.)

On dissection, it was found that the inter-auricular septum was absent, the auricular half of the heart consisting of a single large chamber. The sino-auricular orifice and the entry of the pulmonary vein appeared to be normal in location and structure. The two auriculo-ventricular orifices, though of course inverted in position, were otherwise normal. Viewed from the auricular side, they were separated by a low transverse fold of endocardium representing the sole remnant of the inter-auricular septum. Save for the altered shape occasioned by the inverted situation, and its attachment to the trachea, the ventricle appeared unchanged. The conus arteriosus was of normal structure.

DISCUSSION

What was the mode of origin of the malformation? The possibility presents itself that the heart, otherwise developing normally, underwent version through 180° to reach the inverted position. This interpretation, however, does

not bear close examination. Such version might take place in one of two ways. Version in a sagittal plane around a transverse horizontal axis would result in a reversal of the anterior and posterior surfaces of the viscus; the sinus venosus would come to the front, and the conus would arise on the posterior aspect. This clearly has not occurred. Version in a frontal plane around a vertical dorso-ventral axis, would reverse the right and left sides of the organ and would produce torsion of all entrant vessels. This also has not occurred. The version hypothesis is, therefore, untenable on topographical grounds alone, nor would it suffice to explain the absence of the interauricular septum. It must be concluded, then, that the malformation is a primary developmental irregularity.

The inverted relationship of the auricle and ventricle finds its explanation in the development of the primitive cardiac tube. This structure exhibits five primary regions, which, in caudocephalic order, are the sinus venosus, atrium, ventricle, bulbus cordis, and truncus arteriosus. The atrium subsequently acquires a position dorsal and cranial to the ventricle by folding of the median cardiac tube into a loop, a process clearly described by Keith in his *Human Embryology and Morphology* (1921). In the abnormal heart described, the auricle has retained its primitive position caudal to the ventricle. This condition may be interpreted as due to partial failure of angulation of the primitive cardiac tube, particularly of the important flexure which normally develops at the atrio-ventricular junction. With this fundamental arrest of normal development in the caudal limb of the primitive heart tube may be associated the total failure of the septum primum and the septum secundum, both of which are essentially atrial derivatives. It is noteworthy, however, that the endocardial cushions, which are derived from the atrio-ventricular canal, have developed normally, producing normal auriculo-ventricular orifices.

SUMMARY

An unusual abnormality of the heart of *Tiliqua Scincoides* is described, consisting of (1) inversion of the positions of auricle and ventricle; (2) absence of the inter-auricular septum.

These abnormal features are explicable as due to developmental arrest in the caudal part of the embryological cardiac tube, the auricle retaining its primitive position caudal to the ventricle, and remaining an undivided chamber as in fishes.

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AN UNUSUAL CASE OF ATLANTO-OCCIPITAL FUSION

By H. L. H. H. GREEN

Demonstrator of Anatomy in the University of Cambridge

THE following description of an atlanto-occipital anomaly seems warranted since, although many instances of variation in this region have previously been published, none—with the possible exception of a specimen figured by Corning (1) but not described in any detail—appears to have presented quite the same combination of features as the specimen now under consideration.

I am indebted to Dr Duckworth for the opportunity of examining and describing this interesting condition manifested in a skull which he discovered some years ago in the Romano-British camp at Ashwell. The skull is that of a young woman; it is small and very light owing to the great thinness of the bones, the third upper molars are not erupted and the spheno-occipital synchondrosis has not undergone synostosis. To the under-surface of the left side of the occipital bone is fused, in part, the left half of the atlas.

Macalister (5) distinguished four types of atlanto-occipital fusion and this particular specimen would appear to fall into a subdivision of his Type 2. The posterior arch and the articular process of the atlas are definitely incorporated in the base of the skull but the condition is unilateral. The right half of the bone, though missing, must have been free to articulate with the occipital condyle in the usual way.

Taking the different parts of the left half of the atlas in turn, the following conditions are found to be present:

I. POSTERIOR ARCH

This is incomplete, not reaching the mid-line, and is entirely fused with the margin of the foramen magnum. Its free medial extremity turns abruptly inwards and encroaches to a considerable extent on the lumen of the foramen. Dr Duckworth believes that this inturned piece of the posterior arch may have grooved, and possibly indented, the tonsillar lobe of the cerebellum which would have been moulded on the abnormal margin of the foramen.

II. ARTICULAR PROCESS

The articular process is fused to the occipital condyle but this fusion takes place so much at the expense of the latter that the total depth of exoccipital and articular process on the left side is but little greater than the depth of the exoccipital alone on the right side (fig. 2). There is no distinct foramen for the passage of the first cervical nerve; it may have passed through the canal between the posterior arch of the atlas and the skull which is present

apparently for the purpose of transmitting the vertebral artery, though the lumen of this canal is too small to have allowed the passage of any but an artery considerably below the normal size.

III. TRANSVERSE PROCESS

The transverse process is free from the base of the skull: there is no paroccipital process. A foramen transversarium is present and is bounded posteriorly by a bony bar of normal dimensions. The anterior (costal) lamella,

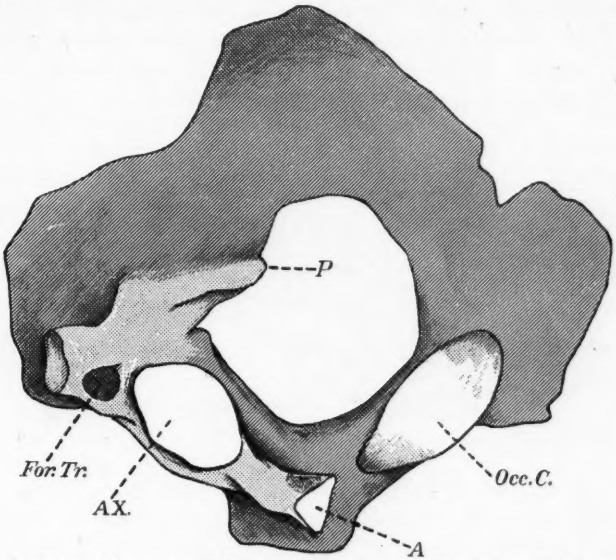

Fig. 1. Ventral view of the specimen described in the text. *A*. The free medial extremity of the anterior arch of the atlas; *AX*. facet for articulation with the axis; *For.Tr*. foramen transversarium; *Occ.C*. occipital condyle; *P*. the free medial extremity of the left posterior arch of the atlas.

Figs. 1 and 2 are reproduced to the actual size of the original specimen.

however, though forming a continuous bar of bone, is extremely thin. The transverse process as a whole is small in comparison with the rest of the bone and only extends for a short distance laterally.

IV. ANTERIOR ARCH

The anterior arch (figs. 1 and 2) is strongly developed and lies in close relation with the basioccipital. It is separated from the latter by a slight though definite interval. The medial end of the arch is free and lies appreciably to the right of the mid-line. The free surface (fig. 1, *A*) is smooth, clearly having been covered with cartilage in the recent state. On the posterior surface of the arch at its medial extremity is a small circular area for articulation with the odontoid process.

V. ARTICULAR SURFACES

The presenting articular surfaces are different on the two sides; on the left side is a typical flat facet for articulation with the superior articular process of the axis, it is slightly ovoid with the long axis pointing forwards and inwards. On the right side is an occipital condyle whose general shape and direction would pass for normal, though its antero-posterior convexity is not so strongly marked as usual. When the whole skull is orientated with the occipital bone *in situ*, it is found that there has been so much absorption in the region of fusion that there is not a great difference in the horizontal level of the two articular facets; the "axial" facet is not more than 3–4 mm. lower than the occipital condyle. The direction of the surface for articulation with

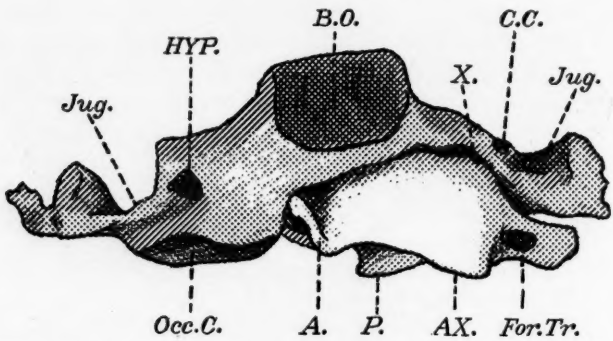

Fig. 2. Anterior view of the same specimen. *B.O.* The surface of the basioccipital which is apposed to the basisphenoid; *C.C.* condyloid canal; *HYP.* hypoglossal canal; *Jug.* jugular notch; *X.* position of the hypoglossal canal on the left side. Other lettering as in fig. 1.

the axis is interesting, it is not only directed downwards and markedly medially but it also faces backwards at an angle of about 30 degrees with the horizontal. It is difficult to imagine what the condition on the right side might have been: there is not sufficient depth available to accommodate the missing half of the atlas without postulating a very marked obliquity for the remaining cervical vertebrae. Possibly the missing half may have been fused with the axis.

VI. FORAMINA

(*a*) The hypoglossal canal lies in its normal position on both sides. It is almost impossible to decide whether the canal was subdivided as the lumen is partly filled with calcareous material; it seems likely that a spicule of bone subdivided it on the right side. It would be reasonable to expect some relationship between the "degree of cephalisation" and the presence or absence of subdivision of the hypoglossal canal: it is noticeable that in every

case quoted by Gladstone and Powell(2), the hypoglossal canal was undivided on the side on which the greater amount of fusion of the atlas occurred. In one of his specimens (VIII) Gordon Harrower(3) describes the first cervical nerve as emerging from the skull in the hypoglossal fossa, thus indicating a still greater degree of fusion.

(*b*) The condyloid canal is small on the left side, opening into the terminal part of the sigmoid sulcus. It is absent on the right side.

(*c*) There is a large foramen transversarium in the transverse process of the atlas, but the canal leading from it to the interior of the skull between the occipital bone and the fused posterior arch of the atlas is very small. On the other hand there is a shallow, though definite, sulcus behind the inferior articular surface on the lower aspect of the lateral mass of the atlas which leads from the foramen transversarium to the foramen magnum. It is possible that this indicates the course of the vertebral artery of the left side which would then have passed below the atlas to reach the interior of the skull. The canal between the atlas and the occipital bone might have transmitted the suboccipital nerve and perhaps the vertebral veins.

DISCUSSION

It can be definitely stated that this specimen represents a case of true congenital fusion; there is no indication of any pathological cause for the abnormal condition. Also there can be no doubt that this is a true assimilation of one half of the atlas with the skull; there can be no question of it being a case of "manifestation of an occipital vertebra."

In the specimen figured by Corning(1) he notes that it showed a marked narrowing of the foramen magnum. This narrowing has already been noticed in the specimen under consideration, though in this case, instead of a uniform constriction of the one side as Corning figures, there is an acute impediment, as it were, in the shape of the free end of the posterior arch of the atlas which juts into the foramen magnum for almost a centimetre.

The separation of the left half of the anterior arch of the atlas from its fellow of the opposite side is interesting. It is a rare condition and has been described in comparatively few cases according to Le Double(4). Presumably, either the anterior arch here had a double centre of ossification with failure of union of the two centres, or ossification may have spread into it from the lateral masses. There is a third possibility, that the right anterior arch element is included in the apparent left half of the bone and has failed to extend laterally towards the right lateral mass: this would account for the free medial extremity of the anterior arch lying somewhat to the right of the middle line. Regnault(6), however, remarks that a slight rotation of the atlas, so that its sagittal plane does not quite coincide with that of the body generally, is a condition to be expected in cases of atlanto-occipital fusion.

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AN ANOMALOUS FACIAL MUSCLE

By J. BEATTIE and F. L. HORSFALL

Department of Anatomy, McGill University

The anomalous muscle here described was found on both sides of the face of a female (white), aged 51, in the dissecting room of the Department of Anatomy in McGill University.

The muscle was a thin band lying immediately below the skin posterior to the angle of the jaw, and passing backwards to be inserted into the superficial fascia and skin over the mastoid process. On the left side the muscle arose from thin fascia attached to the lower 15 mm. of the posterior border of the mandible. Muscular slips arose also from the superficial sheath of the masseter muscle and from the sheath covering the posterior border of the internal pterygoid muscle. The muscle belly made up from these three origins was about 40 mm. long and about 10 mm. wide. The insertion was a triangular fascial sheet attached as described above. On the right side the origin was from the mandible alone. The muscle belly was about 30 mm. long and about 8 mm. wide. The insertion was identical with that on the left.

RELATIONS

The muscle was covered by the skin and superficial fascia. Its origin lay deep to the platysma with which it was not connected. The muscle belly crossed the superficial surface of the gland. Between the muscle and the skin lay a few tributaries of the posterior facial vein. These relations were identical on both sides. (Fig. 1.)

NERVE SUPPLY

On the left side two small nerve twigs were seen to enter the deep surface of the gland. These were found to unite and to form a nerve which joined the main trunk of the facial nerve less than 1 cm. from the stylo-mastoid foramen. No nerve fibres from the posterior auricular branch of the facial nerve or from the great auricular nerve entered the muscle. The muscle on the right side had an identical innervation. (Fig. 2.)

DISCUSSION

Huber (1922–3) has shown that, in the dog, the post-auricular branches of the facial nerve supply not only the adult post-auricular musculature, but also the M. helicis and the M. mandibulo-auricularis. The sphincter colli profundus and its derivatives are innervated exclusively by pre-auricular branches of the VIIth nerve. This part of the superficial facial musculature

is divided in the dog into four parts. The most posterior division—pars auris—is connected intimately with the auricular concha above and meets its fellow ventrally at the middle line of the neck. The pars intermedius lies over the posterior part of the masseteric region, and is also carried to the middle line of the neck. Both parts are supplied by the ramus colli of the VIIth nerve. Amongst the Prosimiae and the Hapalidae, the arrangement is similar to that

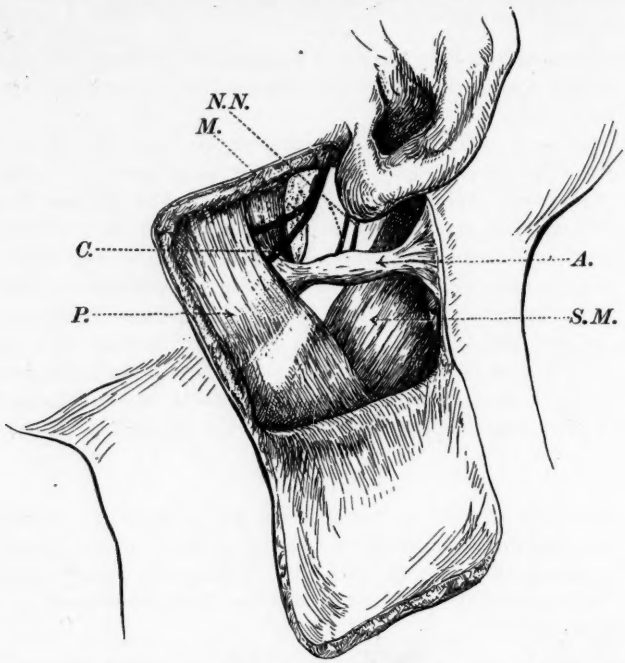

Fig. 1. A dissection exposing the abnormal muscle on the left side. The ramus colli and the ramus mandibularis of the VIIth nerve have been displaced upwards and the lower pole of the parotid gland removed. *A.* abnormal muscle; *S.M.* sterno-cleido-mastoid M.; P. platysma; *C.* ramus colli; *M.* ramus mandibularis; *N.N.* branches of the VIIth nerve to the abnormal muscle.

in the dog. The M. mandibulo-auricularis is supplied by post-auricular branches, and the derivatives of the sphincter colli profundus by pre-auricular branches of the facial nerve (Huber and Hughson, 1926).

Huber (1925) stated that no true representative of the M. mandibulo-auricularis had been found in the higher Primates until then, when he reported an example of this muscle in a macaque. The muscles described by Paugger (1923) as examples of the M. mandibulo-auricularis were considered by Huber to belong to the sphincter colli profundus group because of their pre-auricular innervation. Huber believed that the M. mandibulo-auricularis "has normally

been eliminated from the ground-plan of the facial musculature in the primate group," but the rare M. stylo-auricularis probably represented in man the old M. mandibulo-auricularis.

Edgeworth (1929) challenges, from embryological evidence, the hypothesis of Huber that the M. mandibulo-auricularis is a derivative of the "platysma-sheet" developed from the post-auricular anlage in the nuchal region. Edgeworth considers that the muscle is really a pre-auricular structure and, therefore, may have a pre-auricular innervation, but "the path of its nerve is variable."

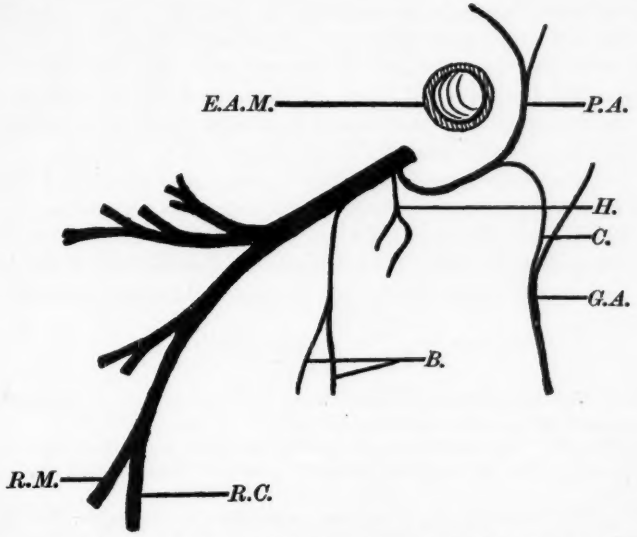

Fig. 2. A diagram of the main branches of the VIIth nerve on the left side to show the relative position of the branches to the abnormal muscle. *P.A.* posterior auricular branch of the VIIth nerve; *C.* communicating branch from the great auricular nerve *G.A.*; *H.* branch of the VIIth nerve to the stylohyoid and the posterior belly of the digastric muscle; *B.* nerve twigs to the abnormal muscle; *R.C.* ramus colli, VIIth nerve; *R.M.* ramus mandibularis, VIIth nerve; *E.A.M.* external auditory meatus.

Le Double (1897) records an example of a muscle in a human subject which he calls an M. auricularis inferior. This muscle was entirely subcutaneous. It arose from the parotid fascia and was inserted into the base of the concha auris. It was innervated by a nerve which left the trunk of the post-auricular branch of the VIIth nerve after this branch had received a twig from the "branche auriculaire du plexus brachial" (*sic*). (It is obvious that Le Double meant the great auricular nerve.)

If Huber's results (1924), obtained by stimulation of the cervical nerves within the spinal canal in the dog and cat, can be applied to man, then it is probable that the motor supply of this anomalous muscle came from the

VIIth nerve. Assuming that this is correct, the anomaly described by Le Double and the anomaly recorded here have different innervations, although their position in the body is strikingly similar. If Huber's general conclusions are accepted, one must be derived from the sphincter colli profundus and the other from a part of the post-auricular musculature which has migrated forwards. If both muscular anomalies are derivatives of the pre-auricular musculature, then the plasticity of innervation hypothesis of Edgeworth would fit the case. When the examples of remnants of the sphincter colli profundus described by Paugger (1923) are compared with the two human examples, it seems most likely that these human muscles are really parts of the sphincter colli profundus, thereby agreeing with Huber's interpretation, but if so it must be admitted that this part of the subcutaneous colli has a variable innervation and that being so, then, as far as the facial musculature is concerned, the Fürbringer theory of muscle homology is no longer absolutely true for terminal innervations from the VIIth nerve.

On the basis of the present evidence it seems most likely that the muscle we have described is a derivative of the sphincter colli profundus.

We are much indebted to Prof. Ernst Huber for a personal communication on the subject of this paper. He expressed the opinion that it was probable that the muscle was "derived from the pars intermedius of the sphincter colli profundus."

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ALVEOLAR AND FACIAL PROGNATHISM

By F. G. PARSONS

A skull of a female Saxon, lately sent to me by W. R. P. Stebbing, Esq., from a grave row cemetery at Finglesham, between Deal and Richborough, has interested me on account of its rather marked prognathism, and has reminded me that I have seen something of the kind before in Saxon skulls.

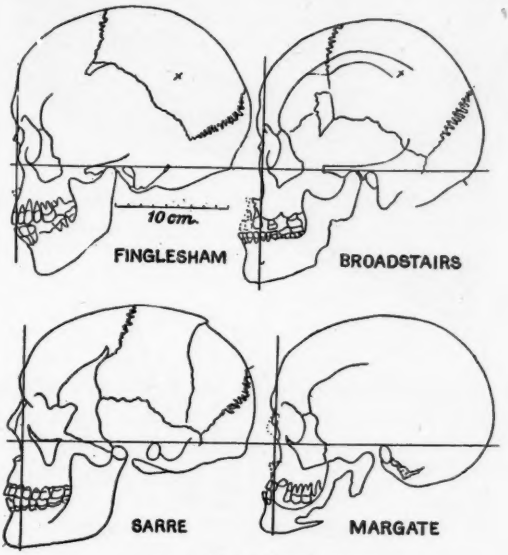

Fig. 1. Jutish female skulls.

Since I have contours, drawn to scale, of over sixty of these[1] I am able to contrast some of them with this Finglesham contour, and to realise that this is a case of marked alveolar prognathism with marked facial metagnathism (if the term be allowed).

It will be seen in fig. 1 that the other female Jutish skulls picked out for comparison combine facial with alveolar prognathism, and I suggest that the line dropped from the nasion, at right angles to the Frankfurt plane, is a useful means of indicating the amount of this latter characteristic. Fig. 2 shows three male Saxon skulls, in which alveolar prognathism accompanied

[1] "Anglo-Saxon skull contours." *R. Anthrop. Inst. Occasional Papers*, No. 9.

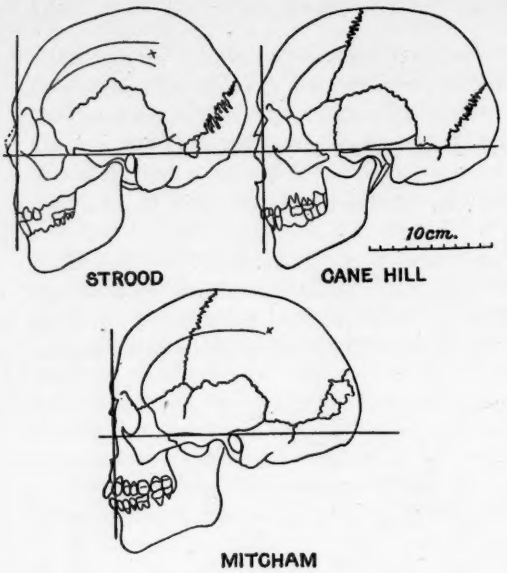

Fig. 2. Saxon male skulls.

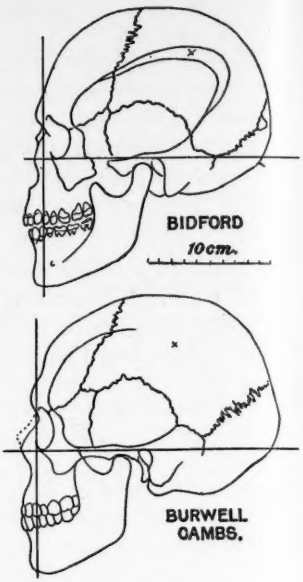

Fig. 3

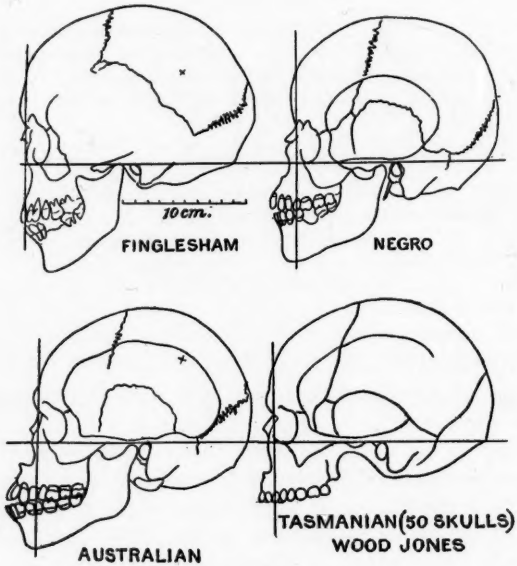

Fig. 4

facial metagnathism, while fig. 3 gives two examples of alveolar, accompanied by slight facial prognathism. Fig. 4 contrasts the Finglesham skull with Negro, Australian and Tasmanian crania, while fig. 5 is a reconstruction,

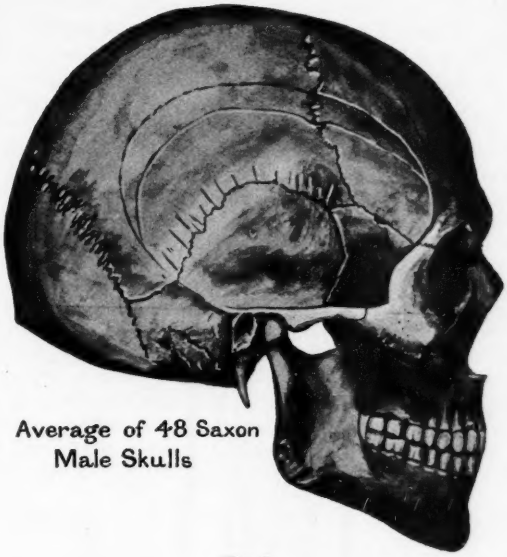

Fig. 5

hitherto unpublished, of forty-eight male Saxon skulls, and shows that slight alveolar prognathism is a characteristic of these people. Whether it is associated with the "edge to edge bite" of Anglo-Saxons I am not prepared to say, but it is worth bearing in mind.

ANATOMICAL NOTE

NOTE ON AN ABNORMALITY IN THE BLOOD VASCULAR SYSTEM OF THE RABBIT

By NELLIE B. EALES, D.Sc. (Lond.)
Lecturer in Zoology in the University of Reading

While dissecting the rabbit in the elementary class, a student was unable to find the right subclavian artery, since no branch was given off from the aortic trunk on its right side posterior to the bicarotid. On investigating further it was found that the specimen exhibited a rare abnormality in this region. The relations of the arterial arches, trachea and vagus nerve are as shown in the diagram. The aorta gives off the

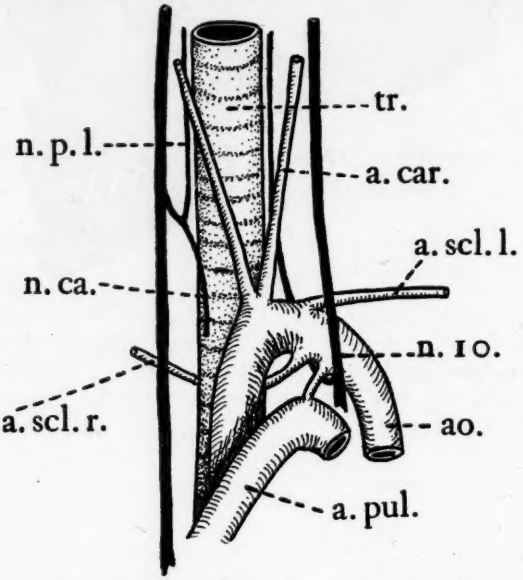

Fig. 1. Abnormal right subclavian artery and right recurrent laryngeal nerve in a rabbit. The aortic and pulmonary arches have been stretched somewhat to expose the ductus arteriosus and right subclavian artery. The trachea is shown but not the oesophagus.

a.car.	carotid artery.
ao.	aorta.
a.pul.	pulmonary arch.
a.scl.l.	left subclavian artery.
a.scl.r.	right subclavian artery.
*n.*10.	vagus nerve.
n.ca.	cardiac branch of recurrent laryngeal nerve.
n.p.l.	recurrent (posterior) laryngeal nerve.
tr.	trachea.

pair of common carotid arteries, then bends to the left, and the left subclavian artery (*a.scl.l.*) issues from it. Posterior to this, but on the opposite side of the aorta, arises the right subclavian artery (*a.scl.r.*) which plunges dorsal to both the trachea and oesophagus on its way to the right arm. The vagus nerve and its recurrent (posterior) laryngeal branch have the normal relations on the left side, i.e. the recurrent laryngeal branch loops round the ductus arteriosus. On the right side, however, the recurrent laryngeal nerve (*n.p.l.*) arises anterior to the carotid fork and does not hook round the right subclavian artery as it should normally do, but passes forwards parallel with the trachea direct to the larynx. A cardiac branch (*n.ca.*) is given off at the bend.

The chief interest in the condition just described lies in the fact that the abnormality must have been embryonic in origin, and arose from disturbance of the arterial arches at about the twelfth day of development. Since the bicarotid and left subclavian are normal, and the abnormal right subclavian is posterior to all these, it appears probable that the growth of the right half of the fourth aortic arch was inhibited for some unknown reason before the limb bud was developed. When later the limb was formed, an offshoot of the aortic arch posterior to the left subclavian artery, and on the wrong side of the aorta arose to supply it. The shifting backwards of the heart and the elongation of the neck during development brought about the elongation of the left recurrent laryngeal nerve, because this branch of the left vagus nerve passed between the aortic and pulmonary arches posterior to the ductus arteriosus, as the direct communication between the arches is subsequently called. On the right side, however, the right recurrent laryngeal nerve was probably formed before the backward movement of the heart occurred and before the abnormal subclavian artery developed. Hence on this side the recurrent nerve is free and is given off unusually high in the neck. Also the one abnormality has brought about the other.

REVIEWS

The Mechanism of the Larynx. By V. E. Negus, M.S. Lond., F.R.C.S. Eng. With an Introduction by Sir Arthur Keith, F.R.S. (London: W. Heinemann (Medical Books), Ltd.) 1929. Sup. roy. 8vo. Pp. xxx + 528. 160 figs. 45*s.* net.

For long the correct appreciation of the functional anatomy of the larynx has been retarded by our conception of that organ as essentially one of voice, and by consequent ineffectual attempts to interpret laryngeal structure almost exclusively in terms of vocalisation.

The full significance of laryngeal mechanism is here presented by Mr Negus in a monumental monograph which constitutes not only a definite enrichment of anatomical literature amplifying our knowledge and understanding of the larynx, but also a notable justification of gross anatomical research and a tribute to the Hunterian manner wherein it was conceived and executed.

This work, the product of ten years' persistent enquiry and original hard thinking, bears the imprint of a cautious mind unravelling, with patient enthusiasm, the evolutionary and functional rôle of a multitude of structural details, reasoning with marked common sense, and advancing novel interpretations of anatomical form with a delightful modesty.

Ignoring pre-conceived notions of laryngeal mechanism and function, the author has carefully and critically traced the evolution of the larynx from its first humble appearance in the Dipnoi to its highest Eutherian elaboration, seeking throughout the underlying principles which govern and modify its structure, investigating its local and general influences in the animal economy, and submitting to the crucial test of experimentation conclusions drawn from the analysis of an extensive range of comparative material.

The collaboration of specialists has been wisely sought for laboratory investigation in the realms of physics, phonetics and pure physiology, whilst embryological and clinical data are freely invoked to confirm the validity of views expressed.

The purposive use of sound as a means of communication and the whole mechanism of phonation are fully discussed, whilst the last chapter details the physiological anatomy of the human larynx—an organ not primarily vocal in nature (indeed degenerate in some respects) but one performing an extremely varied rôle and a convenient handmaid to a brain capable of speech.

The book with its logical command of a wealth of fact and idea is most attractive reading. Each chapter is summarised, and conclusions are drawn therefrom. An Appendix reviews human evolution in the light of laryngeal morphology, the evidence submitted corroborating that derived from the skeletal and cerebral aspects.

An extensive Bibliography would be improved by the dating of all references; an ample Index (with separate index of scientific names) is formed by elaborate Tables summarising the relevant features of species discussed in the text. The volume is handsomely got up; misprints are rare, and the large number of original illustrations most beautifully reproduced.

Those to whom an accurate conception of the larynx and its office is essential—whether anatomists, physiologists, clinicians or teachers of surgery—cannot afford to neglect the evidence and opinions set forth by Mr Negus, for not to know this book is not to know the human larynx.

An Introduction to Physical Anthropology. By E. P. Stibbe, F.R.C.S., Senior Demonstrator in Anatomy at University College, University of London. (London: Edward Arnold & Co.) 1930. 21*s.* 6*d.*

In his treatise on Physical Anthropology Mr Stibbe discloses two objectives. One is the provision of such information as will assist an amateur to appreciate museum specimens representing the course of human evolution or the relations of the human races.

The second aim is perfectly compatible with the first. It has regard to students who are preparing for examination; more particularly the needs of candidates for the degrees of B.A. or B.Sc. in the University of London are held in view, and the schedule expressive of those needs has influenced the arrangement of the book.

Its interest is naturally not limited by such considerations though they require mention if the book is to be appreciated rightly. As a teacher in the premier metropolitan school of anatomy, and as a colleague of Prof. Elliot Smith (to whom he acknowledges his indebtedness for inspiration and advice) Mr Stibbe commands our interest from the outset. The resources of which he disposes are at once apparent, and his work can fairly be regarded as the mirror of the elementary course at University College. As such, and as an introduction to the fuller treatment accorded to particular parts of the subject in Prof. Elliot Smith's *Essays on the Evolution of Man*, his book has an exceptional importance and an assured future.

The actual exposition follows the time-honoured lines of Huxley's lectures on *Man's Place in Nature* with the essay *On the Methods and Results of Ethnology*, observing faithfully the well-known sequence of divisions, viz. those of zoology, of palaeontology and of ethnology (in that order). And where the foundations of treatment are thus orthodox, the details of exposition provide the distinctive features.

Conspicuous among the latter is the prominence accorded to the account of the actual course of human evolution. The student's attention is directed at once to this subject and to the parts played by the brain and by the sense organs respectively. These fundamental considerations are prominent in chapter II, and chapter III is entirely devoted to the brain. The skeleton claims the two following chapters, and then once more the brain is the centre of interest in the summary presented in chapter VI. The latter is illustrated by a diagram of human ancestry confirming those of the *Essay on the Evolution of Man* (1927) and of a letter published in *Nature* on 22 February, 1930.

The section on palaeontology is remarkable for the inclusion of a short account of geology in relation to evolution, together with descriptions of some of the principal types of flint implement. Then follow descriptions of the most important human fossil remains and of *Australopithecus*. The discovery of *Sinanthropus* is recorded, but no description (presumably of the skull) was available at the time of publication.

The ethnological section accords recognition to six human races, and admits eight criteria or features of a physical kind, observable in living subjects. Of these eight features, the shape of the head is placed third in order. In the next chapter (X) specifications of the several racial types are illustrated by figures of the respective skulls, while a coloured map represents the general distribution of those types throughout the world. The last three chapters deal more particularly with definite practical exercises, chapters XI and XII with craniometry, and chapter XIII with anthropometry.

The absence of an account of embryological matters (with the exception of an indirect reference on p. 17) is very striking, but no doubt depends upon the cir-

cumstances influencing the scope of treatment. The curious and irregular blank intervals on the right-hand pages (from 33 to 91 inclusive) are also very remarkable and even perplexing unless the perusal of p. 33 has prepared the reader for their appearance. But even without this aid, the respective page-headings do in fact provide the solution throughout.

The distinctive coloration of certain island groups in the central and eastern Pacific region, and of certain territories in Central America and South America call for explanation or other enlightenment, but the text does not seem to provide these.

Errors of spelling I should correct as follows: for pteryon (pp. 66, 175, 176, 177), read pterion; for phaenazygous (pp. 175, 179), read phaenozygous; for chymotrichous (p. 194), read cymotrichous. And (as regards accents and titles) for Solutre and Saone (p. 115), read Solutré and Saône; for Le Madelein (p. 116), read La Madeleine. As regards dates, for 1909 (p. 128) read 1908. And in the first line of the text on p. 179, the numerals 5 and 4 seem to call for transposition.

I am unable to agree with certain statements as they stand, as for instance the definition of the area of distribution of the Gorilla, which is now well known to exist far to the east of the territory indicated (p. 12). Again, the paragraph (4) on p. 158, seems clearly to refer to typical examples of Negroes, and yet there is a most definite statement that it is "in South Africa, south of the Equator that the most characteristic negro races are seen." No mention is made of West Africa, so that revision seems needed here.

On the side of craniology the existence of distinctions between male and female skulls might be more definitely set forth in connection with the representations of typical racial examples. The contrast between figs. 28 and 29 will perhaps serve to illustrate this point. The same pair of figures brings clearly to light the advantage of uniformity in representation as regards the lower jaw, since beginners will find it difficult to allow for the presence of the mandible in one instance and its absence from the other. Further, the subject of uniformity introduces the consideration of a base-line. The adoption and employment of a fixed base may doubtless be discarded as unsuitable for the purposes of Mr Stibbe's book, and although the "Frankfort" base-line is mentioned, it seems to find no uniform application to the illustrations. Nevertheless I believe that as soon as an observer (whether an amateur or other) turns from the side-view to compare specimens in another standard "norm," he will experience the need for agreement on a standard position. Even a comparison of figs. 38 and 39 is instructive in this connection, should the positions of the coronal suture and the bregma be employed as tests.

In regard to craniometry, a somewhat unexpected result emerges from a scrutiny of the specification of the Mongolian skull (p. 179). The length is described as "rather under 190 mm."—But to comply with the other data as specified, it seems that the length must fall between 175 and 181·25 mm., and a corresponding amendment of the text might be considered. In the anthropometric section (p. 185) the mention of a margin of error of 1 mm. only, probably bears reference to head measurements, since at least 5 mm. must needs be allowed in measurements of larger absolute values.

The contents of the book having thus been surveyed, it remains to repeat the assertion already made as to its assured future, and to welcome it warmly as a notable endeavour to enhance the claims of physical anthropology to fuller recognition than it receives at present.

What is Life? By AUGUSTA GASKELL. (London: Baillière, Tindall & Cox.) 1928. Pp. 324. Price 16*s.* net.

The theory of life here put forward is based on a postulation of certain occurrences in atomic physics. These, it is assumed, were "innumerable," "repeated" and "frequent" in the "early, lifeless earth during geologic time." They were the result of a "critical condition of concentration of ions," giving rise to the production of a new unit, by the close union of a positive and a negative electron. This new unit forms with the atom a "dual-system," becoming itself an intra-atomic system. A series of parallels is drawn between the peculiarities of this dual-system and of the organism, from which it is concluded that the "dual-system describes the organism" and the "intra-atomic system answers to life." The following chapters on "Problems Involved" and "Origin of Species" provide only a very sketchy attempt to fit this theory to the facts of organic life made up largely of quotation from writers of very varying authority to whose works only most incomplete references are given. Finally it is claimed that "while the theory states the cause of cancer, the phenomena of cancer constitute a striking proof of the theory." The book is popular in style, and yet takes for granted an acquaintance with modern physics, and authority is claimed for numerous researchers of merely local reputation.

Anatomical Society of Great Britain and Ireland

PROCEEDINGS

November, 1929 *February*, 1930
May, 1930 *June*, 1930

RECORDED BY
R. J. GLADSTONE

EDITED BY
E. BARCLAY-SMITH

PROCEEDINGS OF THE ANATOMICAL SOCIETY OF GREAT BRITAIN AND IRELAND

THE Annual Meeting of the Anatomical Society was held at St Mary's Hospital on Friday, November 29th, 1929, Professor Fawcett in the Chair.

Mr A. RALPH THOMPSON contributed a paper on "The perineal muscles and urethra in cases of epispadias and ectopia vesicae," of which the following is an abstract:

The question of the presence and functional power of the muscles of the perineum in cases of epispadias and ectopia vesicae is of great importance, and evidence of such is not always forthcoming.

The congenital lesion which is known as "epispadias" is allied to that of "ectopia vesicae," in that both conditions are associated with wide separation of the pubes, and of the lower parts of the two recti muscles. But there is another condition that may be present which connects the one lesion with the other. This is the possible presence of a prostatic urethra.

The following observations were made in order to clear up these points.

Some years ago a specimen of epispadias in a boy, aged sixteen, was dissected. In this case not only were the usual muscles of the perineum existent, but a prostatic urethra was also present.

The vas on each side appeared to open naturally into the urethra in its usual position.

The pubes and adjacent recti muscles were widely separated.

There are in addition two cases of clinical anatomy to be dealt with here:

(1) An infant boy with an ectopia vesicae was subjected to operation, and the bladder was reconstructed.

The operation was a success, but an opening at the base of the dorsum of the penis was left. Through this opening, urine was constantly escaping, and there was no control of the flow of urine.

Two or three years after the first operation a stone was removed from the bladder of the boy. The tip of the stone projected under the base of the penis, and in front of the scrotum. The stone was removed through an incision made in this region on the tip of the stone. The stone was found to be pyriform in shape. It was 4 cm. long, and 22 mm. broad. It was somewhat pear-shaped. The broader, upper part lay in the bladder, and this was separated from the narrower lower part by a well-marked constriction. The lower part terminated in a blunt point.

The stone was circular in section, and strongly suggested that its lower part lay in a prostatic urethra, and that the urethra had terminated in the region of a "compressor urethrae."

(2) A boy aged fourteen presented himself with epispadias. An artificial urethra had been constructed on the dorsum of the penis, but the boy had no control over the flow of urine, which was constantly flowing away. A dissection was made in the perineum, and it was found that there was an excellent "dartos" muscle at the posterior part of the base of the scrotum. There was

clear evidence that the superficial muscles of the perineum were present, and there was a very well marked bulb of the penis which was covered with a well developed "ejaculator urinae" muscle. A curved metal instrument was inserted through the artificial urethra into the bladder, and so turned round that the point of the instrument lay in the bulbous part of the urethra. In this position it was cut down upon. A good prostatic urethra was found, and a permanent opening was made. There was no wound of the mucosa of the bladder or urethra, except that which had been made in connection with the opening. The dorsal urethra was closed. The after-history is most interesting, and important, and well worth the attention of scientific anatomists. Almost immediately after the operation the boy had normal control over the flow of urine through the perineal opening, and was able to hold his water in quite a normal way. He passed his water voluntarily, and deliberately. The epispadias opened again, and the boy once more passed his water this way, and did not use the perineal opening. However, he now had control over the flow of urine, through the dorsal urethra, and was so pleased with this, and the control over the flow of urine that he is averse to further operation. In case he might desire to marry, a passage has been constructed in the position of the normal urethra, which opens at the tip of the glans penis, and this remains patent, though it is not being used for the purpose of micturition. This passage was made, as the author has knowledge of two cases of epispadias, where there was good evidence that the sexual functions were not in abeyance. It is worth notice that the first case, though there are two normal testicles present, has rather the inclinations and pursuits of a female.

The cases that have been cited appear to show that in cases of epispadias and ectopia vesicae the perineal muscles may be present, and capable of performing their proper function, and that a prostatic urethra may also be present. They cannot be disregarded either by the anatomist or the surgeon.

Dr Ida C. Mann made a communication on "The varieties of iris pattern in vertebrates," of which the following is an abstract:

The pattern, formed by the blood vessels of the iris stroma, can be shown to exhibit variations according to the class of animal examined. The pattern, which is typical of mammals, is well known. It consists of a deep layer of arteries and veins united by a capillary plexus concerned with the nutrition of the iris sphincter, and a superficial layer of arteries and veins uniting by direct anastomosis at the circulus iridis minor. This layer is only present in mammals, since it depends for its formation on the existence of a pupillary membrane during development. This structure is absent in animals below the mammals.

In the Sauropsida the iris pattern consists typically of two circumferentially arranged arteries (the inferior and temporal iris arteries) overlaid by a series of radially arranged veins, the two sets of vessels uniting in a circumpupillary capillary plexus. In lizards this plexus is small and narrow. In some birds and tortoises it is extremely large and complex and occupies at least two-thirds of the iris surface.

In Batrachians the circumferential arteries are tortuous and lie superficial to the veins. In some of the tailed Amphibia the arrangement resembles that of the lizards. In Fish the arteries enter on the nasal and temporal sides and are superficial; the veins are deep and are concealed by the argenteal layer.

A demonstration was given of drawings made from living animals in the

Zoo by means of the Gullstrand Slitlamp. The series included, *inter alia*, the following animals: rabbit, guinea-pig, kinkajou, galago, lizard, python, king snake, corvus, starling, owl, eagle, penguin, tortoise, terrapin, axolotl, salamander, frog, toad, teleostean fishes.

Professor ELLIOT SMITH congratulated Miss Mann on the excellent series of coloured lantern slides which she exhibited.

Professor PATTEN enquired whether there was any striated muscle fibre in the iris. Some birds, e.g. the parrot, appear to have the power of contracting the pupil at will.

Professor E. FAWCETT exhibited a reconstruction model of the lower jaw and adnexa of a 17 mm. human embryo, a description of which will be published in the *Journal of Anatomy*.

Dr R. H. HUNTER communicated two papers of which the following are abstracts:

(*a*) *The development of the human vagina.*

The vagina is known to be developed from a solid cord of cells, but the origin of this cord is doubtful. One view, advanced by Tourneux and Herrman in 1886, states that the epithelial cells of the primitive genital canal, formed from the fused lower ends of the Müllerian ducts, differentiate into two zones. According to this view, the cells of the lower zone change into stratified squamous cells, and by their proliferation fill the lumen of the lower half of the primitive canal, completely occlude it, and form the solid cord of cells from which the vagina is developed. Wood Jones in 1924 brought forward another view: that the Müllerian ducts at an early stage lose their connection with the urogenital sinus, and that two solid cords of cells arise from their lower ends, and that these tunnel their way to the exterior. The vaginal cord is, according to this view, a new structure.

As the result of a study of twelve wax-plate reconstructions of the pelvic region of human embryos up to the third month, and of dissections of 120 foetuses from this period to birth, a modification of these views would appear desirable.

At the 32 mm. stage of development, the lower end of the simple tube, formed by the fusion of the lower ends of the Müllerian ducts, terminates blindly at the urogenital sinus. The lumen of the tube extends to this point. The sinus end of the tube develops a bulbous-like growing-end, and this protrudes into the posterior wall of the urogenital sinus. In the 42 mm. stage a short solid cord of cells extends between the lower end of the primitive genital tube and the sinus, and the lumen of the canal no longer reaches the lumen of the latter. As the embryo increases in length the solid cord of cells also increases in length, until the 142 mm. stage is reached, when a series of irregular lateral growths develops at the sinus end. These growths continue; they soon involve the whole of the cord, rapidly run together and by the 150 mm. stage form a single solid cord. By the breaking down of the central core a lumen, the vagina, is formed. The solid cord of cells from which the vagina is formed is therefore a cord which was in direct continuity with the epithelium of the sinus from the beginning, and is not a new growth as suggested by Wood Jones. The last part of the vagina to be formed is the fornix. This first appears as two wing-like upgrowths around the lower end of the primitive uterus, one in front and one

behind. The dorsal wing appears first and remains throughout development larger than the ventral. Both wings are well marked at the 367 mm. stage. The central cells of these two wing-like growths break down and the lumen thus formed forms the depression known as the fornix.

(*b*) *The foetal cervix uteri.*

Attention was drawn by Scammon in 1926 to the fact that if a chart be made of the length of the foetal uterus at different stages of development, the growth curve will show a sudden drop immediately after birth. In checking over these growth measurements of the foetal uterus in the present investigation it was noted that the cervix and body of the uterus do not appear to develop at the same rate; that the cervix at an early stage rapidly assumes a relation to the body of the uterus quite different from that seen in the normal non-pregnant uterus of the adult. Separate measurements were then made of the cervix and body of the uterus, and it was found that the sudden reduction in length of the uterus after birth was due to a sudden reduction in size of the cervix uteri rather than a reduction of the length of the uterus as a whole.

A similar enlargement of the cervix uteri is known to occur in the cervix of the adult pregnant uterus. The enlargement of the foetal cervix is thought to be due to the same causes as act on the adult: namely that the placental hormones act on the cells lining the cervix and cause an enormous secretion of mucin which in turn collects in the lumen of the cervical canal as a distinct plug. The cells of the epithelial lining of the canal certainly show definite evidences of activity. At the 147 mm. foetal stage the cells are of a low cylindrical type with a centrally placed nucleus and a small amount of cytoplasm. But in the foetus of 341 mm. length the cells have become of a high cylindrical form with a large amount of cytoplasm and a basal nucleus. In the newly born infant the cells return to the condition before the enlargement of the cervix, that is to a low cylindrical type with a centrally placed nucleus.

Mr J. F. Rogers contributed an exhibition of a cinematograph film of "Gastro-intestinal movements." This was demonstrated to the Society by Professor William Wright.

Dr F. Davies showed a series of lantern slides demonstrating the position and connections of the bundle of His in birds. The paper will be published *in extenso* in the *Journal of Anatomy*.

Professor J. P. Hill enquired what the proportion of Purkinje fibres in the bird's heart was as compared with that of a mammal.

Dr Davies replied that the fibres in the bird's heart were not surrounded by a definite sheath like that in the calf or sheep, they were therefore not so conspicuous as in the mammalian heart in which they were aggregated in a definite bundle. Owing to their more diffuse disposition in the bird, it was difficult to estimate the proportional number of fibres as compared with that of the mammalian heart.

Dr H. A. Harris read a paper on "The joints in relation to the costal cartilages," which will be published in the *Journal of Anatomy*.

Professor Le Gros Clark said that the process of ossification which was described as taking place in the rib cartilages of Man, was to be regarded as a calcification rather than a true bone formation.

Dr R. J. GLADSTONE demonstrated a reconstruction model of the brain and cranial nerves of a 20 mm. human embryo, a description of which will be submitted for publication in the *Journal of Anatomy*. He commented on the large size and thin walls of the arteries supplying rapidly growing parts such as the developing brain and optic vesicle. The main arteries on the surface of the growing brain, owing to the thinness of their walls, resemble veins, and their diameter is two to three times that of the extracranial parts of vessels from which they spring, namely the vertebral and internal carotid arteries.

Dr S. ZUCKERMAN read a paper on the "Menstrual cycle of primates." This will be submitted for publication in the *Journal of Anatomy*.

FEBRUARY, 1930

AN ordinary meeting of the Anatomical Society was held at the London School of Medicine for Women, on Friday, February 7th, 1930. The President, Professor Bryce, in the Chair.

Dr P. N. B. ODGERS demonstrated a series of reconstruction models of the "Pancreas from human embryos," a description of which will be published in the *Journal of Anatomy*.

Professor J. P. HILL remarked with reference to the question of the existence of two ventral pancreatic outgrowths in the human subject that Dr Tribe had demonstrated the presence of two ventral pancreases in the Marsupial, but in the rabbit the ventral pancreas arises as a single outgrowth.

Professor J. FLORIAN, introduced by Professor J. P. Hill, read a paper on "the Development of the connecting stalk in early human embryos." The paper will be published in the *Journal of Anatomy*.

The PRESIDENT remarked that the series of embryos described by Professor Florian showed a fairly complete sequence in the early phases of development of the human embryo, and that our interpretation of the development of certain structures might, as our knowledge of intermediate stages becomes more complete, require revision and redescription. There appears to be a considerable degree of variability of such structures as the amnion stalk, which is present in one embryo and not in another and he had always been doubtful whether the allantoic diverticulum is not a later development than is usually supposed.

Mr A. J. E. CAVE contributed a paper entitled "Further observations upon the inferior grooving of the first rib."

Some time ago attention was drawn in the *Journal of Anatomy*, vol. LXIII, Pt 3, April 1929, to the frequent occurrence of certain grooves (*sulci diagonalis et transversus*) impressed upon the inferior surface of the first rib by the various branches of the first intercostal nerve. These markings were encountered in over 50 per cent. of a series of 190 disarticulated first ribs, the material examined comprising (*a*) modern English and European bones, and (*b*) ancient Egyptian remains covering a long interval of time (3000 B.C.–A.D. 600); the grooves were not met with in a short series of disarticulated gorilla and chimpanzee ribs.

Observations have since been extended to material from various ancient and modern races of mankind and to a much more extensive anthropoid series. The rich collections of human comparative anatomy in the Hunterian Museum of the Royal College of Surgeons were kindly placed at my service by Sir

Arthur Keith. Professor Elliot Smith afforded me ready access to valuable material in the Institute of Anatomy, University College, and additional material was gleaned from the various sources indicated below. The results of investigations are presented in tabular form for the sake of brevity. In the human series, none but disarticulated skeletons were examined, their final number appearing rather small owing to the absence of the first ribs from many of the skeletons worked through. No racial affinity is implied in the grouping of the various present day races, the arrangement being one of mere convenience. In the anthropoid series, in addition to disarticulated material, very careful scrutiny was made of the pleural aspect of the thoracic operculum in a number of mounted skeletons (see Table IV) with exactly similar negative results. Both first ribs were present in all the anthropoid skeletons examined, whether articulated or not.

(N.B. In the following tables, Abs. = rib missing; Ft. = faint marking; + = grooving present; 0 = absence of grooves.)

Table I. *Human—ancient races*

(Identification numbers refer to the *Cat. Roy. Coll. Surg. Mus.*)

Race	No.	Sex	Age	Grooving: Right rib 1	Grooving: Left rib 1
Ancient Egyptian mummy. No date	583 C	♂	Ad.	+	+
Do. IV Dynasty	A 583 g	—	*c.* 18	+	+
Do. Ra-Nefer. Memphite noble of V Dynasty, *c.* 2700 B.C.	583 D	♂	Ad.	Abs.	0
Do. Middle Empire	7/169	♂	Ad.	+	+
Do. Ptolemaic	1265/12	—	—	Abs.	+
? Sumerian. Separate and complete burial. Tel-el-Obeid, near Ur. First half 3rd millennium B.C.	—	?♂	Ad.	++	Abs.
Guanche. Desiccated body from ancient sepulchre, Teneriffe	566	♂	Ad.	0	0
Romano-British. From tile-cist, Wetherby, Yorks., about 4th cent. A.D.	Leeds Anat. Dept.	♂	Ad.	+	Abs.
Anglo-Saxon. From Newbury	350/32	—	Ad.	+	Abs.
Do. From Newbury	317/24	—	Ad.	+	Ft.
Do. From Thetford	—	—	Ad.	Abs.	++

Table II. *Human—present day races*

Australian aboriginal	1045	?	Ad.	+	+
,,	1066	?	Ad.	+	+
,,	1083·2	?	Ad.	+	+
New Hebrides native	1149 A	♂	Ad.	+	+
African bushman	?	♂	Ad.	++	+ mod.
,,	1300·15	?	Ad.	0	0
,,	1300·16	♀	Aged	0	0
,,	1300·18	♂	Ad.	Abs.	++
Veddah	680 A	♂	Ad.	Abs.	0
,,	680 B	♂	Juv.	Abs.	++
Borneo native	733	♂	Aged	+	++
Andaman islander	1209	?	Ad.	+	+
,,	1479 BD	?	Ad.	+	+
,,	1207	♂	Ad.	++	++
,,	1212	♂♀	Ad.	?+	?+
,,	1216	♀	Ad.	0	0
,,	1218	♀	Ad.	0	0
,,	1215	♀	?	0	+
,,	1475	?	Ad.	Abs.	++

Table II (*continued*)

(Identification numbers refer to the *Cat. Roy. Coll. Surg. Mus.*)

Race	No.	Sex	Age	Grooving: Right rib 1	Grooving: Left rib 1
Hindu	674·5	?	Ad.	0	0
,,	674·6	?	Ad.	Abs.	+
,,	674·17	?	Ad.	+	+
,,	636 D	♂	Ad.	+ Ft.	+ Ft.
,,	636 E	♂	14	+ Ft.	0
Punjabi	631 A	♂	Ad.	Abs.	++
,,	635 A	♂♀	36	+	+
,,	—	♀	60	+	++
Gowallah	635 C	♂	?	0	0
,,	635 B	♂	38	+	0
Kabul native	630 A	♂	c. 30	0	0
Sikh. Lahore	631 B	♂♀	40	0	+
Bhutan native	652 B	♀	Ad.	0	0
Chinese	691 A	♂	40	0	Abs
Lapp	554	♂	Ad.	+	0
Eskimo	836	♂	Juv.-Ad.	+ Ft.	?
South American native slave	1236	♀	Ad.	trace	Abs.
Chatham islander	765	?	Ad.	+	+
Negro	1257 Aa	♂	30	0	0
Maldive islander	674 A	?	?	+	+

Table III. *Anthropoid—disarticulated*

	No.	Sex	Age	First rib: Right	First rib: Left
Chimpanzee (10).					
Univ. Coll. Lond.	L 3	—	Juv.	No evidence of inferior grooving	
,,	L 4	—	Ad.		
,,	CA 13	—	3–4		
R.C.S. Mus.	3	—	Ad.		
,,	4	♀	Ad.		
,,	5	♀	Ad.		
,,	6	♀	Ad.		
,,	14	—	Juv.		
,,	15	—	Juv.		
Prosect. Zool. Soc.	—	—	Juv.		
Gorilla (10).					
Univ. Coll. Lond.	L 1	♂	Ad.	No evidence of inferior grooving	
,,	L 2	—	Baby, 2 mths.		
,,	L 5	—	Baby, few mths.		
,,	L 6	—	Imm.		
,,	L 7	—	Imm.		
,,	L 8	♂	Baby, 8 mths.		
R.C.S. Mus.	21	♂	Ad.		
,,	21 A	♂♀	Ad.		
,,	24	♀	Ad.		
Orang (9).					
R.C.S. Mus.	38 A	♂	Ad.	No evidence of inferior grooving	
,,	40 A	♂♀	Ad.		
,,	40 E	♂	Young Ad.		
,,	47	♀	Juv.		
,,	51	♂	Juv.		
,,	52	—	Juv.		
,,	53	—	Baby		
,,	54 A	♂	Juv.		
,,	54 B	♂	Juv.		

Table IV. *Anthropoid—articulated*

	Sex	Age	First rib	
			Right	Left
Chimpanzee (4).				
Leeds Museum	—	Imm.	No evidence of inferior grooving	
Manchester Museum	—	Imm. Ad.		
Univ. Sheffield, Anat. Dept.	♂♀	Ad.		
" "	♀	Ad. 7½ yrs.		
Gorilla (8).				
Univ. Sheffield, Anat. Dept.	—	Baby	No evidence of inferior grooving	
" "	♂♀	Ad.		
" "	♂♀	Ad.		
Sheffield Museum	♂	Ad.		
Leeds Museum	—	Imm.		
Univ. Coll. Lond. (CA 4)	♂♀	Imm.		
" (CA 5)	♂♀	Ad.		
" —	♂	Ad.		
Orang (6).				
Univ. Sheffield, Anat. Dept.	♂	Ad.	No evidence of inferior grooving	
Sheffield Museum	—	Imm. Ad.		
Leeds Museum	—	Ad.		
Univ. Coll. Lond. (CA 21)	—	Ad.		
" (CA 22)	—	Juv.		
" (CA 23)	—	Ad. 15 yrs.		

It is evident from these tables that inferior grooving of the first rib is common to the several races of mankind, both past and present. Within any given race, all the customary variations of this feature are to be observed in a little over a half of the number of individuals examined. When the first rib is thick and robust, the markings tend, though not invariably, to be absent. Despite the close approximation to the human type manifested by many chimpanzee first ribs, e.g. in the possession of an attempted *sulcus subclaviae* and of a rudimentary scalene tubercle, in no case was inferior grooving detected in any anthropoid rib. Such grooving appears to be confined to Man (of whose first rib it constitutes a normal anatomical character), and herein lies its main interest. Of itself, this grooving is trivial, being but one expression of the effect of the forelimb upon the axial skeleton. Considered as an example of a secondary marking upon a bone, present in Man but absent from the anthropoid, it stimulates speculation and requires more explanation.

It may be that the anthropoid thoracic operculum is more functionally active than the human, that, in consequence, the same intimate relationship of the intercostal nerve to the first rib does not obtain, and that therefore no secondary nerve markings are produced.

On the contrary, it is very likely that the neuro-osseous relationships in the first intercostal space are actually much the same in man and in the ape (although I have yet to verify this by actual dissection) and, if such be the case, the absence of secondary markings from the anthropoid bone is puzzling.

Mere thickness of the rib will not alone account for this absence, since bony tissue can offer no great impediment to the course of nerve fibres anywhere in the body. Other things being equal, one might expect a more pronounced nerve marking in the thicker bone.

The solution to the problem probably does not lie locally. Throughout the entire skeleton a similar state of affairs is evident. The human bone, rich in a great variety of secondary markings, presents in its elegance of sculpture a remarkable contrast to the clumsier and much less informative anthropoid bone. Indeed, osteoclastic activity would appear to have reduced the gross

quantity of osseous tissue in the human skeleton to a satisfactory minimum, which minimum, in virtue of its secondary markings, affords mute testimony of much relative anatomy. The same "refining" process does not occur in the anthropoid: whether because of the demands of greater muscular activity or because of the rôle played by the endocrine organs, it is impossible to say.

Too little is known as yet regarding the growth of bone and the mutual reactions of this tissue with the tissues of other systems, and a vast field of study in this regard awaits exploration.

Professor LE GROS CLARK remarked that the extent of grooving of the first ribs by the first thoracic nerve had been shown to be due to the degree of obliquity of the thoracic operculum.

Mr H. A. HARRIS said that the early fusion of the manubrium with the body of the sternum was associated with the large size of the upper limb, which required a rigid support.

Professor WRIGHT mentioned the fact that the retrahens aurem, although a small muscle, produced a very marked groove on the human temporal bone; whereas in the elephant in which the muscles are very large, the markings on the bones are slight. The distinctness of the grooves and muscular ridges seen on bones was dependent on some other factors than the pressure of vessels and nerves and the traction of muscles.

Professor G. ELLIOT SMITH read a paper on "The influence of the development of the macula on the cortex," which is to be published in the *Journal of Anatomy*.

The President, Professor WOOLLARD, Professor WRIGHT and Professor LE GROS CLARK joined in the discussion. Professor Woollard said that the question of representation of the macula lutea in the telencephalon, which is supplementary to its representation in the mid-brain, could only be answered by a special study of the cortical structure of the area striata. Professor Le Gros Clark remarked that there was a distinction between two parts of the area striata in those monkeys which have a macula lutea, and those in which it is absent. Professor Wright referred to the initial work of Gordon Holmes and Lister in locating the macula in the occipital pole, and the arterial supply of this region partly by the middle cerebral artery and partly by the posterior cerebral artery, the latter vessel supplying the area on each side of the calcarine fissure.

Professor WOOLLARD made a communication on "The cutaneous glands in man," which will be published in the *Journal of Anatomy*.

Three groups of glands were distinguished:

Sebaceous; Sweat—(*a*) Epicrine, (*b*) Apocrine. The apocrine glands are sebaceous glands which have lost their connection with the hair follicles and, finally, open on the surface. The apocrine glands were not more abundant in the Australian aborigines than in other races.

Professor WRIGHT asked whether it was possible to distinguish any differentiation of function between the epicrine and apocrine glands.

Professor HILL said that the cells of the epicrine glands appeared more granular. The apocrine resemble the sebaceous glands. Ordinary sweat glands may open into the hair follicles. Epicrine glands do not normally open into the follicles.

Professor WOOLLARD, in reply to Professor Wright's question, said that it was difficult to distinguish any difference in function between the two types of glands. There seemed to be a definite relationship between the activity of the cutaneous glands in general and the sexual organs.

Mr C. P. G. WAKELEY contributed two specimens for exhibition which were shown by Professor Blair.

(1) An aortic valve with a supernumerary cusp discovered at a "post-mortem" examination of an individual who had shown signs of cardiac disease.

(2) A case of stenosis of the duodenum, from an infant who lived 9 weeks. The part of the duodenum behind the constriction and the stomach were greatly dilated.

Mr N. ASHERSON, introduced by Mr H. A. Harris, read a paper on "The surgical anatomy of the premastoid space." The paper will be published in the *Journal of Anatomy*.

Mr HARRIS, Professor LE GROS CLARK, Professor WRIGHT and Professor FRAZER took part in the discussion. Mr Harris stated that the petrosquamous suture may remain open up to the age of 65 years. It was questionable whether the suture afforded the easiest passage of pus to the surface. Mr Asherson said that there was a difference in this respect between adults and children. In children the oedema is often premastoid in position and not over the mastoid process. The latter was sclerotic in about 20 per cent. of cases. Professor Le Gros Clark enquired whether Mr Asherson regarded the sclerotic condition as a normal variation or a pathological state. Mr Asherson said that there was a considerable variation in the density of the bone in perfectly normal conditions.

MAY, 1930

AN ordinary meeting of the Anatomical Society was held at the Middlesex Hospital Medical School on Friday, May 2nd, 1930, Professor Walmsley in the Chair.

Mr C. G. PAYTON read a paper on "Measurements of the diaphyseal growth in the limb bones of the pig." The paper will be submitted for publication in the *Journal of Anatomy*.

Mr A. J. E. CAVE demonstrated two cases of congenital deformity of the cervical vertebrae.

(1) *A further case of fusion of the third and fourth cervical vertebrae.*

Some time ago (*Proc. Anat. Soc.* Feb. 1929) two specimens of fusion of the third and fourth cervical vertebrae from the Leeds Anatomy Department were exhibited before this Society. By courtesy of Professor J. S. B. Stopford, photographs are now shown of a further example of such fusion in the Manchester University Anatomical Museum. These illustrate very clearly the anterior, posterior and left lateral aspects of the specimen, which itself is not available. The fusion is not pathological in nature; there is no osteophytic distortion of the two vertebral bodies, no ossification of capsular or common ligaments, and no osteo-arthritis of the articular surfaces themselves. Those which are visible (the upper of C.V. III and the lower of C.V. IV) are clean cut

and well defined, and those facets involved in the fusion appear to have been equally free from disease of any kind.

Both vertebrae possess well-formed bodies (separated in life by an intervertebral disc) and vigorous transverse processes showing the customary characteristics. Fusion has occurred between the greater part of the two neural arches—the articular pillars and laminae being united—the pedicles and tips of the spines remaining distinct; all interarticular and interlaminar structures are absent. The mingling of neural arches is perhaps a little more pronounced on the right side than on the left, although the components of the composite arch are easily recognisable bilaterally.

The fusion is most likely of congenital origin. This is the probable explanation not only from the general appearance of the specimen and from the absence of any secondary changes, but also because this region (C.V. III) of the column is not uncommonly the site of manifestation of errors of vertebral segmentation. At the same time, since coalescence has occurred in the region of the fibrous tissue plane between the two vertebrae, the possibility of a postnatal production cannot be definitely dismissed.

Le Double (*Traité des Variations de la Colonne Vertébrale, etc.*, 1912) was quite familiar with the "synostose congenitale" which occasionally manifests itself between the third cervical and either its cephalic or its caudal immediate neighbour. Genuine congenital fusions of the axis with C.V. III are not infrequent. A large series (about 30) of such cases will be the subject of a future communication. Examples of congenital fusion of C.V. III and IV alone are of much rarer occurrence, less than half a dozen being recorded in the literature on the subject. Apart from cases already mentioned, the following are of interest:

A full-time female foetus dissected by Le Double in 1873 exhibited vertical median division of the body of C.V. IV; the right moiety was free, but the left was fused above to C.V. III and below to C.V. V.

In an anomalous adult male spine described by Brash (this *Journal*, XLIX, 1915, p. 243), now in the Leeds Anatomy Museum, the vertebral formula was C. $6\frac{1}{2}$, D. 13, L. 5, S. 5, Co. 4. The right half of C.V. IV was congenitally absent and an asymmetrical composite piece resulted from the fusion of the persistent left half of C.V. IV with C.V. III above and with C.V. V below. On the right C.V. III and V were fused.

The Anatomy Department of University College, London, contains an excellent example of cervical vertebral fusion—apparently congenital in nature. The third cervical is intimately fused (by body and by neural arch) both to the axis above and to the fourth vertebra below. All parts of the several vertebrae are present.

Le Double (*op. cit.* p. 46) makes mention of an adult female skeleton in the Museum of the University of Sassari, Sardinia, in which the bifid extremities of the spinous processes of C.V. III and IV are so fused as to enclose a foramen.

(2) *Deformity of the cervical spine.*

This specimen, of combined anatomical and physiological interest, is kindly loaned by Professor A. F. Dixon from the Anatomical Museum, School of Anatomy, Trinity College, Dublin. It is the cervical column from an adult male (T.C.D. Cat. No. 34), with some deformity of the basis cranii, the precise nature of which is not recorded. The sacrum is not preserved, but the twelve

thoracic and the five lumbar vertebrae are normal and typical, being quite free from any signs of osteo-arthritis or other bone disease.

The neck bones have suffered changes due to static rather than to infective causes, resulting (when articulated) in so pronounced an exaggeration of the normal cervical curvature, that the ventral median plane of the upper cervical spine lies at 45 degrees or more to that of the lower four vertebrae, whilst the atlas looks backwards rather than upwards.

The second and third intervertebral discs have disappeared; the seventh cervical vertebra is normal in all respects, the sixth (saving its spine) nearly so. All the cervical bodies, with their corresponding transverse processes, retain their customary size and features, although the subaxial processes lack their usual inclination and stand out at right angles to their respective vertebrae. There is synostosis of C.V. IV and V by both bodies and neural arches.

Posteriorly, the neural arches (save those of C.V. VII) exhibit departures from the normal as a result of the marked hyper-extension of the cervical spine.

There is mal-development of each arch and spinous process together with secondary changes (compression, absorption, fusion, etc.) due to pressure. The laminae of the axis are feeble and are crowded down upon the much compressed and absorbed subjacent arches, wherein great destruction of articular surfaces, together with the formation of adventitious joints, is manifest. Excluding their pedicles, the arches of C.V. IV and V are synostosed, the depth of their confluent laminae not exceeding the ordinary depth of a single lamina. It would appear that the unusual and grave degree of hyper-extension resulted in the mid-cervical vertebrae (III, IV, V) being caught between the downthrust of the head and upper cervical spine and the upthrust of the thoracic and lower cervical spine with the consequent vertebral fusion and secondary laminar changes indicated. Abnormal neck posture from an early age has inhibited full development of spinous processes—that of C.V. VII alone being unaffected. The axial spine is rudimentary—a mere asymmetrical non-bifid median knob—whilst the subaxial spines lack the median, dorsally directed element, though preserving their bifid tips, now irregularly disposed.

The cervical nerves together with their ventral and dorsal primary divisions have escaped involvement in the secondary changes affecting the vertebrae.

The posterior atlantal arch is mal-developed. Where it lodges the vertebral artery it is 7 mm. wide only, whilst elsewhere it measures 3 mm. approximately in any direction. Its posterior tubercle is absent.

The stunted superior articular facets (15 mm. × 11 mm.) are almost plane, and are bounded anteriorly by a furrow for fibres of the capsular ligament.

Movement was evidently much restricted at the cranio-vertebral articulation.

No osteophytic invasion of fibrous tissue can be detected anywhere in the specimen. C.V. I, II, VI and VII have clean articular facets. Changes on the under surface of the axial laminae and in the laminae of C.V. III, IV and V must be interpreted as pressure phenomena and as pathological in that sense.

The whole spine demonstrates the dominance of function over form, and the close interdependence of the two.

Professor T. Walmsley demonstrated an abnormal heart in which the aorta was situated in front of the pulmonary artery. There was thus a transposition of the aorta and pulmonary artery. The interventricular septum was

fused with the septum intermedium more to the left than the right. The specimen confirmed the suggestion made by Sir Arthur Keith, that the bulbar part of the cardiac tube becomes incorporated in the upper part of the ventricles. The condition appeared to be due to a reversal of the spiral division of the pulmono-aortic canal, the distal end remaining unaffected, the lower end being reversed.

Professor T. B. JOHNSTON said that he had seen a somewhat similar case of congenital cardiac deformity.

Professor WOOLLARD spoke of the capability of the developing heart to adapt itself to changed conditions, there seemed to be an inherent potentiality of development in each ventricle. He doubted whether there was any connection between these cases and complete transposition of the viscera. Professor Walmsley agreed with Professor Woollard and said that the condition was one which only affected the ventricular loop.

Professor FRAZER concurred with Professor Walmsley's explanation of the condition being due to a reversal of the spiral septum in the pulmono-aortic canal. The left bulbar ridge had grown backward.

Professor BARCLAY-SMITH remarked on the fasciculation in the interior of the ventricles, and the adaptive power of one ventricle to perform the function normally carried out by the other.

A full description of the case will be published in the *Journal of Anatomy*.

Dr P. N. B. ODGERS showed a skull, the occipital bone of which exhibits some abnormal markings for the venous sinuses. Apparently, from the character of these grooves, the superior longitudinal sinus divided just above the internal occipital protuberance into a right lateral and a large left occipital sinus, the latter being continued, as an equally large left marginal sinus, to the jugular foramen. There is no marking for the medial five-sixths of the transverse part of the left lateral sinus. This groove first appears immediately above the commencement of the sigmoid portion. On the other hand, this sigmoid groove is only slightly smaller than that on the right side. Further, on the left side of the vertex there is a very deep channel for a middle meningeal sinus, which opens above into a lateral lacuna. This lacuna has so eroded the bone over it, that there is a small oval perforation of the skull in this situation. The skull came to the Department of Human Anatomy at Oxford as part of a half-set of "Students Bones."

Miss GWLADYS LLEWELYN demonstrated a series of reconstruction models illustrating the form of the spleen at various developmental stages. The paper will be published in the *Journal of Anatomy*.

Professor FRAZER, speaking with reference to the date of appearance of the splenic fissures, stated that they certainly may occur in embryos earlier than the 22 mm. stage.

Dr R. J. GLADSTONE and Mr C. P. G. WAKELEY made a communication on "Rudimentary first thoracic and cervical ribs," considered from the etiological and clinical standpoints. The subject was introduced by Mr Rutherford on behalf of Mr Wakeley. He referred to the production of pressure symptoms, which are said to occur chiefly in cases in which there is a post-fixed brachial plexus. These symptoms are motor, sensory or vasomotor in type. The median as well as the ulnar nerve may be involved. The symptoms are both subjective

and objective. The vascular changes are due not so much to pressure on the subclavian artery as to pressure on the vasomotor fibres carried in the first dorsal nerve. Lantern slides of X-ray photographs from cases operated on by Mr Wakeley were shown, and cases contrasting the conditions of rudimentary first thoracic ribs, and seventh cervical ribs were demonstrated by Dr R. J. Gladstone, who pointed out the frequency with which these anomalies are associated with other defects such as: fusion of vertebrae, half vertebrae, congenital scoliosis or spina bifida. He considered that the very frequent association of these defects with the presence of rudimentary first thoracic ribs and cervical ribs indicates that there is a common cause for the two conditions, namely a disturbance of the normal processes of segmentation, which takes place at an early stage of embryonic life.

Professor WOOLLARD commented on the discrepancies which sometimes occur in individual cases which show prefixation of the limb plexuses in one region of the body and post-fixation in another. These and the cases shown certainly indicated a disordered segmentation involving both skeletal and neural systems. In the Mayo Clinic he had seen cases treated by tenotomy of the scalenus anticus muscle. Mr Warren Low had reported a case in which there was wasting of the opponens pollicis and in which the medial cord of the plexus was affected.

Mr CAVE said that in an examination of 220 subjects he found cervical ribs in one only, indicating a percentage 0·45. Others had estimated their frequency as high as 1 to 2 per cent.

Mr J. M. FLOWER, introduced by Professor D. M. Blair, demonstrated an example of accessory soleus muscle, a description of which will be published in the *Journal of Anatomy*.

Professor YEATES mentioned that he had seen a similar case.

Professor FRAZER remarked that the plantaris muscle is a part of the soleus, and that it grows upwards from its insertion. It may pass either in front of or behind the soleus, and he considered that the position of an accessory muscle lying deeply to the soleus, did not exclude its origin from the plantaris.

Professor LE GROS CLARK read a paper on the "Thalamus of tarsius," which will be published in the *Journal of Anatomy*.

JUNE, 1930

AN ordinary meeting of the Anatomical Society was held at University College on Friday, June 20th, 1930. The President, Professor Bryce, in the Chair.

Professor C. J. PATTEN exhibited a model of an abnormal heart in a human embryo.

This model has been reconstructed from the heart of a human embryo which measured 2·4 mm. C.R.L. The chorionic vesicle was complete and measured 1 cm. in diameter. The uterus from which it was obtained, after removal by operation from a living patient, was placed in formalin without delay. The reagent was rather on the strong side, and the preparation lay for several months before being cut; hence some allowance must be made for shrinkage. Sections of the embryo were cut at 10 μ, and a wax-plate model reconstructed in the usual way. Here I must acknowledge my indebtedness

and best thanks to Dr M. B. Lavery formerly Senior Demonstrator in Anatomy in the University of Sheffield. The model indicates that the embryo had reached a stage in which the neural tube is closed, there are two dorsal aortae, and a tubular notochord. The heart has assumed the contour of a capacious pipe, curved like the letter S. The myocardium only is here represented, but a reconstruction of the endothelial tube showed that it was demarcated into the five primary chambers, including the auricular canal. The auricular chamber is still undivided.

The feature of interest in this specimen is the strange manner in which the whole cardiac mass appears to have rotated beyond the normal about a central axis: consequently, the auricle has been carried, not only well to the left, but even in front of the ventricle. Here then is presented the developmental basis of a form of dextro-cardia, because further and continued growth would suggest that the right auricle would take its place behind and even to the left of the ventricular axis, while the left would lie quite in front. In such a case the apex of the ventricle would occupy a position to the right of the middle line, and the origins (but not the eventual relations) of the two aortae would be reversed, that is considering the question from the standpoint of topographical anatomy.

Professor D. M. Blair demonstrated a skull (with skull-cap missing) in which the groove for the right lateral sinus was completely absent and also the groove for the superior longitudinal sinus up to the level of the saw-cut. (Knott, *Journ. of Anat.* vol. xvi, mentions cases of great reduction of the superior longitudinal sinus whose usual tributaries drained into the inferior longitudinal sinus; and other cases where the straight sinus received the termination of the superior longitudinal sinus, which did not groove the occipital bone for the last inch of its course.) The groove for the left lateral sinus was unusually large; the fossa for the left jugular bulb burrowed extensively upwards into the petrous temporal bone, deep to the inner wall of the middle ear. A pair of enlarged left mastoid foramina were present.

In a second skull shown, both lateral sinuses had evidently drained to an unusual degree through enlarged mastoid foramina. The fossa for the left jugular bulb was very small. No direct knowledge of the soft parts in connection with either of these skulls was available.

A third skull exhibited was part of a specimen, shown by Dr Gladstone at the previous meeting of the Society, of rudimentary first thoracic ribs associated with abnormal cervical vertebrae and torticollis. There was a marked uprising of the cranial bone in the region of the occipital condyles and the basi-occiput. The lateral masses of the atlas in consequence appeared to have interfered with normal drainage through the jugular foramina—completely on the left side, partially on the right side. Both mastoid foramina were enlarged—the left foramen had provided the sole outflow for the left lateral sinus. The soft parts had been dissected in this case, and the left jugular foramen was seen to transmit the ninth, tenth and eleventh cervical nerves only.

Dr R. J. Gladstone demonstrated a loose body in the peritoneal cavity. A description of this specimen will be submitted for publication in the *Journal of Anatomy*.

Professor J. Florian showed sections of early human embryos, including the Fetzer, Beneke, Bittmann I, T.F., Bi. 24, Bi. II, Bi. III, and Bi. XI.

Dr A. Girgis exhibited models illustrating the development of the heart in the rabbit.

Miss C. J. Hill showed preparations and drawings of nerve-endings in reptilian skeletal muscle.

Dr E. P. Stibbe read a paper, illustrated by lantern slides, on "Afferent fibres of the eye muscle nerves."

In a previous paper (*Proceedings*, vol. lxiv, Pt 1, Oct. 1929), it was shown that definite communications existed between the third, fourth and sixth nerves respectively and the ophthalmic division of the fifth; that the histology of these communicating branches was in harmony with that of "sensory" fibres in contrast with that of true motor fibres; and that in certain cases ganglion-cells were found in the course of the communication.

During the past year the investigation has been continued, the work to date being almost exclusively morphological. Mr Stibbe expressed the opinion that morphological methods should be exhaustively applied before embarking on experimental.

Examinations were carried out on the following material: Human adult cavernous sinus. Human full-time foetus cavernous sinus and orbit. Cavernous sinus of embryos of rabbit, pig, marsupial (perameles). Cavernous sinus and orbit of adult monkey, cat, dog.

Slides were shown to illustrate the following conclusions:

(1) The communications previously described are confirmed. They have been demonstrated in the orbit (adult cat and human full-time foetus) and in the cavernous sinus (human full-time foetus, rabbit and perameles embryo).

(2) Microscopically these are true communications; the fibres can be traced from one nerve into the other. Slides were shown to illustrate this, as well as one graphic reconstruction (pig embryo) and one wax-plate reconstruction (full-time human foetus).

(3) The ganglion cells are not constant. All the early embryos examined showed a number of cells on the sixth nerve. Some cells were found on the third nerve in certain cases only; no cells were found on the fourth nerve in any case. The third and fourth nerves communicated in most of the early embryos either with the Gasserian ganglion or with the developing ophthalmic division of the fifth nerve.

(4) The next step is a study of the cells constituting the so-called nucleus of the mesencephalic root of the fifth nerve. These cells have been studied morphologically by Meynert, Golgi, Merkel, Kolliker, Cajal, Weinberg, Johnston and others with contradictory results. They have also been studied experimentally by May and Horsley, Johnston and others. Opinion is divided as to their nature, and as to the likelihood of their being connected with the motor-nerves of the eye.

The speaker showed slides of Edinger tracings and photos demonstrating that these cells were bipolars in some cases and unipolars in others. In either case he believed them to be functional bipolars closely resembling the cells of the Gasserian ganglion and of posterior root-ganglia.

(5) It was then demonstrated that these cells have intimate relationship to the motor nuclei of the third and fourth nerves, not merely in position, but in that one long process of the cells could be traced into the root of the motor-nerve.

(6) It is therefore suggested that the cells of the mesencephalic root of the fifth, of the Gasserian ganglion and in some cases the wandered cells found in the motor-nerves themselves, all belong to one afferent, possibly proprioceptive system of the eye-muscles.

(7) Experimental work has been begun on the lines of looking for chromatolysis after section of eye-muscle nerves. Two results were shown, but this side of the case is in a tentative position, and will be proceeded with. It is hoped subsequently to publish a full report of the morphological and experimental work.

Professor BEATTIE communicated a paper on the "Oculo-motor nerve." This was based on experimental work, involving stimulation of muscle-spindles in a cocainised muscle, and section of the eye-muscle nerves and fifth cranial nerve with subsequent histological examination of the degenerated tracts. The paper will be submitted for publication in the *Journal of Anatomy*.

Professor ELLIOT SMITH, referring to the statement made by Professor Beattie that the proprioceptive fibres of the fifth cranial nerve pass entirely by the third cranial nerve, mentioned that Sherrington, by cutting the fifth nerve, found that no change occurred in the tone of the muscles. The mesencephalic root of the fifth cranial nerve may contain proprioceptive fibres for the muscles of mastication.

Professor J. P. HILL and Professor J. FLORIAN made a communication on "The head-process and prochordal plate in early human embryos." The paper will be published in the *Journal of Anatomy*.

The PRESIDENT said that the problem of the nature of the prochordal plate, was a question of Comparative Embryology. The part in front of the gastrulation zone had been termed the acrogenetic region of the embryo. It was a question whether the cavities found in this region were "head cavities". It is possible that their occurrence might be explained by tension in this part of the blastoderm. A cavity was present in the specimen he had himself described.

Professor FLORIAN said that the problem was rendered more difficult by the circumstance that no one had a complete series of specimens, and that some of the specimens were imperfectly preserved. The head process was much longer in some specimens than in others.

Professor J. CAMERON gave a lantern demonstration illustrating some of his series of Craniometric Memoirs, No. III–VII. Memoir No. III is to appear in the October number of this *Journal*. Memoir No. IV will be submitted for publication in this *Journal* sometime next year. He demonstrated the variations that take place in the proportions of the "superior gnathic triangle" and "inferior gnathic triangle"[1] in the Eskimo, Mongol, Negro and European skulls; also in fossil Crania, the Gorilla, Tarsius and the Chimpanzee. The gnathic triangles afford an accurate measure of the degree of prognathism which may be easily estimated and recorded graphically. Professor Cameron also gave a summary of a paper in which he demonstrated that the "interorbital width" is greatest in the Negro, smallest in the Eskimo and intermediate in white races.

[1] The "superior gnathic triangle" is bounded by lines joining the nasion, subnasion, and basion.

The "inferior gnathic triangle" is bounded by lines joining the subnasion, alveolar point and basion.

Dr A. MacConnaill read a paper on the "Trabecular musculature of the right ventricle" which will be submitted for publication in the *Journal of Anatomy*.

Professor Popa and Miss Una Fielding communicated a paper on the "Vascular connections of the pituitary body." The paper is to be published in the *Journal of Anatomy*.

Sir Arthur Keith commented favourably on the value of the method of investigation by serial sections, and stated that injection experiments had failed to fill the vessels. The interest of this sinusoidal "portal" system lay in the meaning of the blood current directed from the pituitary to the infundibulum. He enquired whether or no any colloid material was found accompanying the vessels?

Dr F. Davies and Dr E. P. Stibbe showed dissections and drawings to illustrate certain points in the descriptive anatomy of the intercostal nerves.

(1) As shown by Professor Walmsley, as long ago as 1916, these nerves do not lie in the plane between the internal and external intercostal muscles, but deep to the internal intercostal. They are separated from the pleura by a musculo-fascial plane consisting from behind forwards of subcostal muscles; intracostal muscles and fascia (Walmsley); triangularis sterni muscle and fascia (sterno-costal fascia).

(2) Each intercostal nerve gives off near the angle of the rib a large collateral branch, resembling the branch of the artery. This crosses to the upper border of the rib below, occupies the same plane as the main nerve, and is distributed to the deep plane of muscle, including the diaphragm and transversus abdominis in the case of the lower six nerves.

(3) Certain nerves have apparently anomalous courses, namely the second and the seventh. The second runs in the posterior half of its course not in the second space but along the upper border of the second rib. The seventh when it approaches the subcostal margin leaves the seventh intercostal space to cross the seventh cartilage on its deep aspect, and to emerge at the subcostal margin from the sixth space.

In view of the fact that at least the proper plane of the nerves has long ago been described, it is surprising that text-books still give the old statement that the nerves lie between the two intercostal muscles. It is proposed to carry the study of the descriptive anatomy of these nerves a little further; and it is hoped to publish suggestions for a complete amended description of them.

Professor G. Elliot Smith demonstrated a cast of Sinanthropus, a description of which will be published later.

Dr A. Basir, introduced by Professor J. P. Hill, read a paper on the "Spleen of *Echidna*."

Dr F. Davies communicated a preliminary note on the "Conducting system in the monotreme heart." The paper will be submitted for publication in the *Journal of Anatomy*.

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THE NON-METRICAL MORPHOLOGICAL CHARACTERS OF THE SKULL AS CRITERIA FOR RACIAL DIAGNOSIS

PART I

GENERAL DISCUSSION OF THE MORPHOLOGICAL CHARACTERS EMPLOYED IN RACIAL DIAGNOSIS

By FREDERIC WOOD-JONES
Honolulu

It is a matter of common experience that in dealing with crania of different racial types an impression of racial affinities and differences may often be intruded by an aggregation of apparently insignificant morphological features that are not capable of measurement or even of precise verbal definition or assessment. We are aware of these ill-defined racial peculiarities, and their obtrusion into the field may conceivably influence our judgment in assigning a racial diagnosis to a skull; but if they should receive a definite sanction as affording valid evidence of racial affinities is a point upon which anthropological teaching is silent. Even if we accept the common sub-division of cranial characters into metrical and morphological features we do not achieve a complete classification of the significant structural modifications of the skull. It is true that certain features, such as length and breadth of the cranium, may be measured with considerable precision and the measurements may be made in virtual agreement with various recognised conventions. We may, therefore, term such characters metrical; but it is the constant despair of the physical anthropologist that neither absolute measurements nor even indices, no matter how cunningly contrived, can give a satisfactory concrete picture of the form of the cranium or of any part of it. Of the characters that are incapable of precise measurement all are not alike, for some are capable of reference to conventional standards and some are not. Even the accepted conventions of verbal estimation are far from satisfactory in their actual application. It is true that any bony feature may be described as being large or small, present or absent, according to its degree of development or prominence. It is also true that these conditions may be defined, not by the estimation of the observer alone, but by reference to standard charts or scales depicting the different degrees of development to which individual descriptive terms should be applied. But in actual practice two factors militate against the attainment of any real scientific accuracy by the employment of this method. In the first place the examination of any series of skulls will, despite the most resolute attempts to adhere to a conventional standard, lead to the creation of special criteria within the limits of the series under review. It is difficult to attain to that

detachment from present conditions that refuses to describe as "well developed" the maximum manifestation of a character within the series, even though this maximum manifestation may actually be only "slightly developed" when the comparison is made with the standard laid down in some commonly accepted scale. Concerning this group of characters Hooton (1926) has remarked that "they are capable of classification according to presence or absence, grade of development and form, if the observer is experienced and is able to maintain a consistent standard for his morphological appraisals." It is readily agreed that a moderate amount of experience will ensure fair consistency within the limits of a series, but to carry over the standard adopted in one series to an altogether different racial type is a feat difficult of attainment by most physical anthropologists.

The second difficulty that is encountered in attempting any sort of metrical valuation of these characters is the fact that there is the impossibility, even when the most precise regard is had for conventional standards, of divorcing any individual feature from its surroundings. A bony eminence may appear prominent by reason of the conformation of the surrounding parts even when by actual individual measurement it fails to attain to a development that could rightly be denoted by any such term. This is so even with such features as glabella prominences, mastoid processes and other conspicuous cranial characters for which graphic scales have been laid down by Broca and others: it is more strikingly the case with minor features such as the pharyngeal tubercle, post-glenoid tubercle, the spine of the sphenoid and many others. It is in regard to these apparently minor characters that the anthropologist is left without any guide; and if they are to be dealt with at all they needs must be treated by means of some form of verbal description. Such descriptions are nearly always unsatisfactory, their utility being almost entirely confined to their employment as working notes by their original author.

It is obvious that all the minor features of cranial architecture that are not susceptible of metrical treatment are not of sufficient morphological importance to warrant any very precise attempts at verbal description. Many of them are purely adaptive and so are of little or no value in assisting in the diagnosis of racial or tribal characteristics. But many are non-adaptive and, like the similar features in the skulls of lower Mammals, are of the utmost importance in diagnosing the characters of individuals belonging to minor groups. The difficulty is to ensure agreement as to which are non-adaptive and so worthy of attention and which are purely adaptive and so comparatively valueless in racial studies.

Hooton has paid some attention to this question and has selected the following as being, in the main, non-adaptive cranial features: (1) the sutural pattern, (2) the post-glenoid tubercle, (3) a pharyngeal fossa or tubercle, (4) the form of the incisor teeth, (5) the presence of prognathism. This list, as Hooton states, is by no means exhaustive and one of the features—prognathism—is in some degree capable of metrical treatment. Every physical anthropologist will have

his own ideas as to what characters are and what are not of importance, and the present paper aims at calling attention to their diagnostic value as a general thesis rather than to assigning ultimate importance to any individual characters.

Probably one of the greatest needs of physical anthropology at the present time is some definite attempt to employ more fully such non-adaptive features as are incapable of precise measurement or even of standardisation by existing methods, but which yet have a high value in diagnosis and assessment of different types of human crania. Only in this way may the study of the human skull be rendered in any way comparable to the system by which zoologists are accustomed to assess the zoological position and affinities of the lower Mammals by regard to their cranial characters. The present author, feeling that the future study of racial affinities is not destined to develop in the direction of the elaboration of systems of measurement or of the refined mathematical treatment of measurements, has here made an attempt to apply these more distinctly zoological methods to the study of the racial characters of human skulls.

Before attempting to describe the actual condition of these minor morphological features present in any particular type of human skull it is essential to determine their characters in the skulls of generalised Mammals as well as in those of the more specialised types present among the higher Primates. Certain of these features as they occur in lower Mammals are illustrated in a series of labelled figures and no elaborate descriptions are therefore needed (see figs. 2–10). The figures are included for the further purpose of explaining the nomenclature employed and this is a point of some importance. Descriptive physical anthropology has suffered much by the loose employment of such terms as simian, negroid and, worse still, anthropoid, which, with others of their kind have, for lack of proper definition, caused endless confusion. When a feature of the human skull varies in a direction which directly resembles the condition typical of and peculiar to the members of the catarrhine series it is here termed *pithecoid*, and, when used with this definition the term will commonly stand in contrast to *primitive*. No ideal scheme is intended to be laid down in this short paper. The features that the writer has been in the habit of noting in examining series of skulls are submitted without selection. It is only by further work in this direction that we may arrive at what might be termed a sufficient descriptive catalogue of non-metrical cranial morphological features, which, combined with graphic reconstruction methods, may be expected to yield a concrete picture of the essential characters of any racial type of skull.

(1) *Cranial Form.* The nomenclature introduced by Sergi, but in its initial simplicity rather than its high elaboration, is probably most satisfactory: and where necessary simple qualifying adjectives are employed in connection with the original primary names of distinctive forms.

(2) *Cranial Asymmetry* is recorded from inspection of the norma verticalis and as such it may (*a*) fail to be apparent to the eye; be conspicuous to a vary-

ing degree either as (*b*) a *normal* (left occipital prominence) or (*c*) *reversed* (right occipital prominence) asymmetry. Although the full implications of cranial asymmetry are not known, there appears to be some evidence that approximate symmetry is primitive, and that normal asymmetry is associated with the skilled use of the right hand.

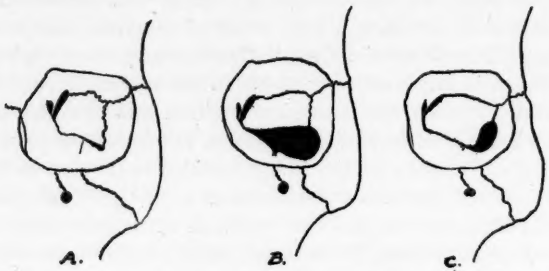


Fig. 1. Forms of the sphenomaxillary fissure. *A*, narrow; *B*, wide; *C*, narrow with expanded extremity.

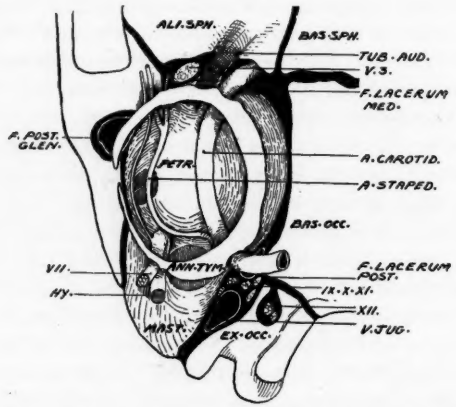


Fig. 2. Hypothetical condition of the posterior portion of the base of the skull in a generalised mammal.

(3) *Sutures.* The form of the sutures is included by Hooton among the non-adaptive characters of the skull, and it at least is certain that the sutural pattern shows very distinctive features in different series of skulls. For this reason some form of description is essential in routine work. The topographical nomenclature of Frederic and Oppenheim appears to be the most convenient and precise, and for degree of complexity Broca's scheme, with perhaps the verbal expressions of linear, very simple, simple, complicated, highly complicated, substituted for the numerical grades 1, 2, 3, 4 and 5.

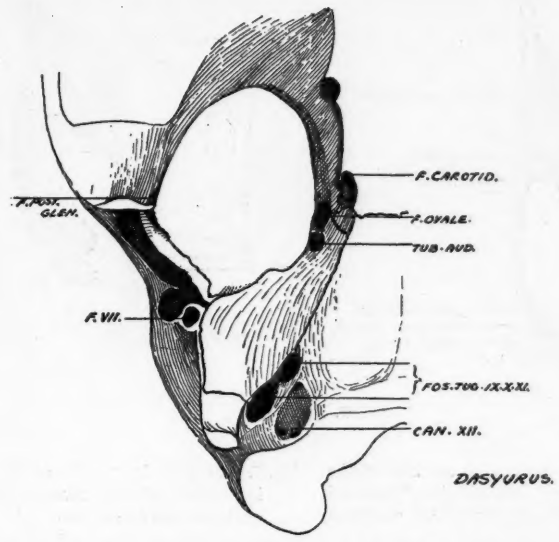


Fig. 3. The posterior portion of the base of the skull in a didelphian mammal (*Dasyurus maculatus*).

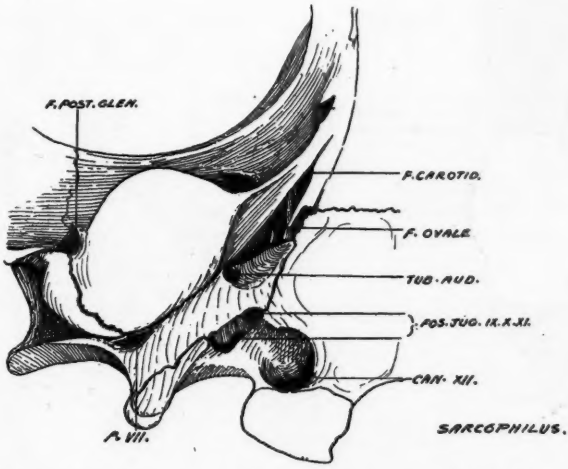


Fig. 4. The posterior portion of the base of the skull in a didelphian mammal (*Sarcophilus ursinus*) in which a "pterygospinous" bar gives lateral exit to nerve v. 3. Compare with Fig. 7.

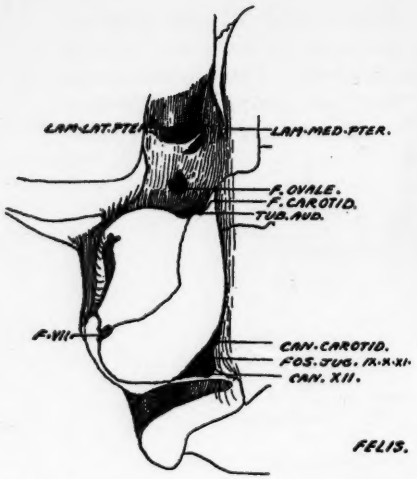


Fig. 5. The posterior portion of the base of the skull in a "lower" monodelphian mammal (*Felis cattus*). Note the completed condition of F. ovale.

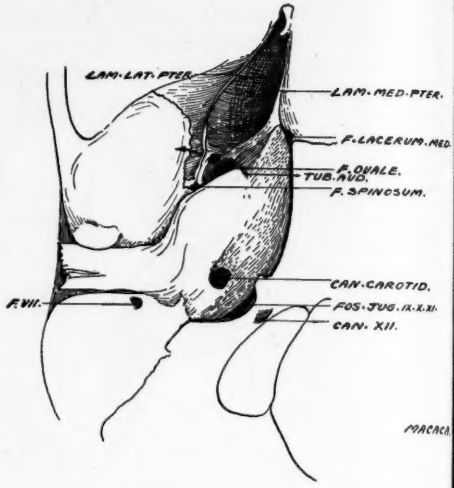


Fig. 7. The posterior portion of the base of the skull in a haplorhine (*Macacus rhesus*). Note the incomplete F. ovale and the lateral bar.

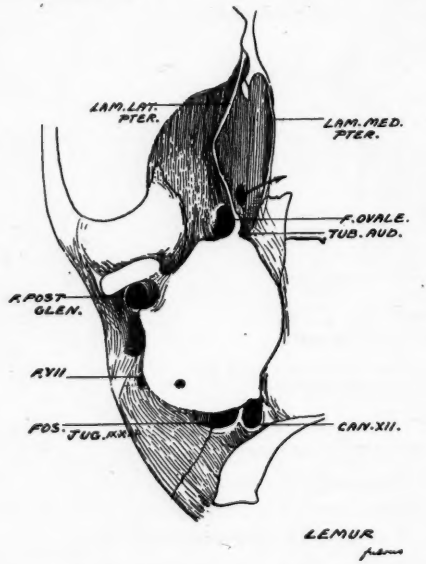


Fig. 6. The posterior portion of the base of the skull in a strepsirhine (*Lemur fulvus*). Note the completely enclosed condition of the F. ovale and the median bar, and compare with fig. 7.

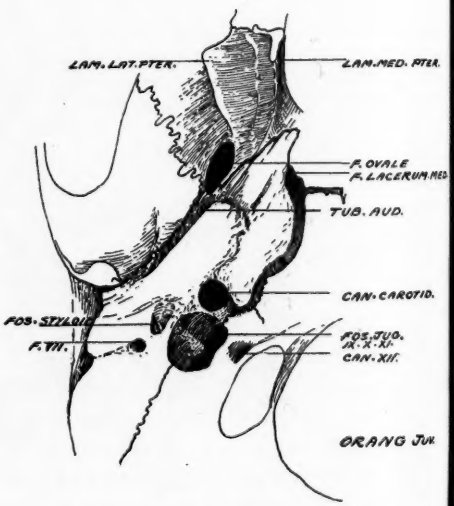


Fig. 8. The posterior portion of the base of the skull in an orang.

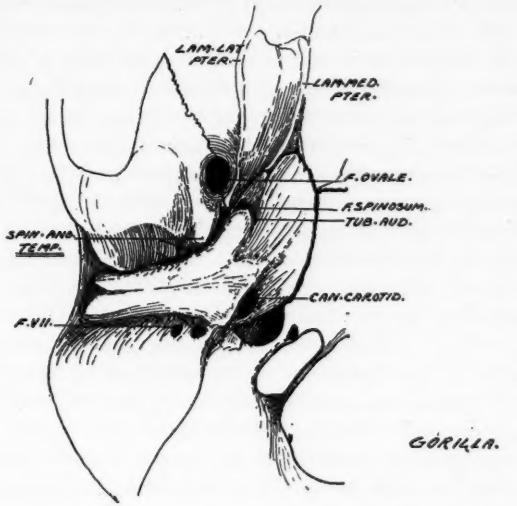


Fig. 9. The posterior portion of the base of the skull in gorilla. Note the peculiar gorilloid conditions of the position of F. ovale and the development of a spina temporalis simulating a spina angularis sphenoidei.

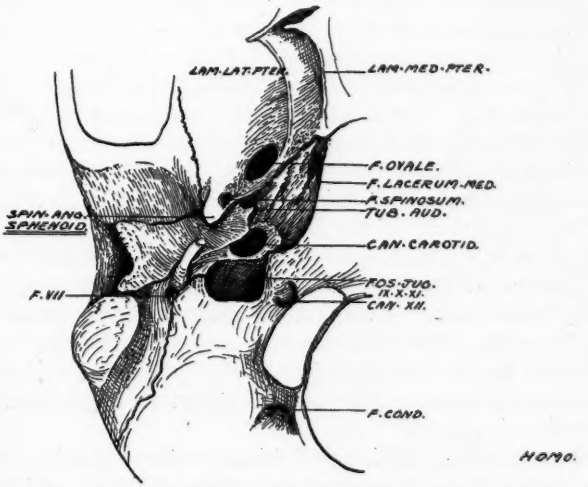


Fig. 10. The posterior portion of the base of the skull of homo. Compare with fig. 9.

(4) *Ossa Suturarum* are localised by Frederic's nomenclature and their size recorded by Broca's standards in which small, medium and large may be used as alternatives to grades 1, 2 and 3, 4 and 5.

(5) *Type of the Pterion* is recorded as normal when a wide alisphenoid parietal contact is present; as normal but narrow when the contact is 5 mm. or less; as stellate when (as very rarely) all four bones appear to be in contact on the outer surface at a central meeting point; and as pithecoid when the pattern is definitely reversed and the temporal makes contact with the frontal.

(6) *Epipteric Bones.* Apparent temporo-frontal contact effected through the intervention of a definite epipteric bone is recorded as such and in addition to this the number and site of all epipteric bones is noted.

(7) *Supraorbital Foramina, Notches or Grooves.* The human peculiarities and racial variations in these features are well known. Additional markings, ranging from complete foramina to mere grooves, such as the notch or foramen of Henle (F. frontale) are probably also of certain racial significance.

(8) *Foramen Ethmoidale Anterius.* In the typical human conditions this canal has its orbital exit between the lower margin of the pars orbitalis of the frontal and the upper margin of the lamina perpendicularis of the ethmoid. It is a pithecoid variation for the canal to pierce the frontal altogether above the suture line.

(9) *The Sutures of the Inner Wall of the Orbit.* The meeting of the frontal and the maxilla between the reduced ethmoid and the lachrymal is a pithecoid variation, and as such is noted when it occurs.

(10) *The Spheno-maxillary Fissure.* As Duckworth has noted, the typically human feature of a wide spheno-maxillary fissure is a condition more primitive than the narrow fissure characteristic of the pithecoids. The fissure may be linear, narrow, moderate or wide. Or it may have the form of a narrow or moderate slit with a greatly enlarged lateral extremity (see fig. 1).

(11) *The Form of the Orbit.* The most striking racial features in the shape of the orbit consist in the varying degrees of the obliquity of its transverse axis. Theoretically this obliquity is capable of precise measurement; but in practice attempts at determination of the angle of obliquity are not successful. In these circumstances recourse must be had to a mere visual estimation derived from examination of the skull strictly in the norma facialis. Crude though this method may be it is one that should be employed in routine work and its findings should be incorporated in all descriptions of racial types of skull.

(12) *Infra-orbital Foramen.* Great variety exists in the suture line which indicates the course of the infra-orbital nerve during its passage from the orbital floor to the shelter of the infra-orbital canal. The typical pithecoid condition is for the foramen to be multiple rather than single whereas in *Homo* the single orifice is normal.

(13) *The Form of the Jugal.* Subdivision, partial or complete, of the jugal assumes a restricted racial value when dealing with local Pacific problems. Apart from subdivision there exists the widest range of racial variation in the

form of the jugal. The bone may be massive or slight. Viewed from the norma facialis the lateral margins of the two bones may appear more or less parallel or the lower margins may be widely everted.

(14) *Nasal Bones.* Separation of the two bones by a suture line except in old age is typical of *Homo.* Fusion at an early age is pithecoid. The breadth of the naso-frontal articulation is subject to some racial variation and the relative contribution of right and left nasal bones to this articulation is also variable.

(15) *The Narial Aperture.* Apart from the well-known metrical expressions of the form of the narial aperture there are several features of considerable importance which are not capable of measurement or mathematical treatment. As with the contour of the cranial vault, measurements of the narial aperture give no indication of the very characteristic variations in the actual shape of the object measured. The orifice may be pyriform, ovoid, oval, almost parallel sided or more or less circular in outline.

The narial margins are of extreme racial importance and their condition should always be included in routine work. The aperture may be bounded by a single sharp margin which constitutes a sharp ridge separating the narial cavity from the superior alveolar surface. This sharp margin may, or may not, culminate in the development of a prominent spina nasalis anterior. The margin may be single and yet not be represented by an edge that is sharp and linear, the narial cavity then being separated from the superior alveolar surface by a well-developed, but rounded, ridge, usually without the development of a spina nasalis. The bounding edge may be double instead of single at the lower limits of the aperture. The two ridges may be equally well developed and may run with but little separation towards the site of the spina nasalis, or the ridges may be more widely separated, or the outer one may be well defined and the inner one faint, or *vice versa.* The separation of the two ridges may increase and their prominence diminish until a defined gutter, included between the two lines, may open from the floor of the nasal chamber to the face. As a culmination from this stage the floor of the nasal fossae may be in continuity with the facial surface of the maxilla without the intervention of any continuation of the lateral narial margin. This last condition is primitive, and here, exceptionally, the terms primitive and pithecoid express a similar condition.

(16) *The Nasal Septum.* Unfortunately in every long series of skulls the septum is so commonly damaged at its anterior end that its recording can only be carried out in a comparatively small number of cases. Primitively the septum is perpendicular and in some races this primitive condition is frequently retained; far more frequently it is deflected to one side or the other, and it is not impossible that the frequency and the type of the deflection may have some significance.

The Region of the Foramen Lacerum Medium. The subdivisions that have taken place in the primitive generalised foramen lacerum medium have led to many changes, which have been rather varyingly effected in different

mammalian types and have led to some interesting features of human cranial morphology. These features are treated individually.

(17) *Foramen Ovale.* Primitively the foramen is merged in the foramen lacerum medium and in this case the mandibular division of the trigeminal nerve passes through the interspace between the alisphenoid and the petrous. In the foramen lacerum medium the nerve lies to the lateral side of the tuba auditiva and the main entocarotid artery, and to the medial side of the arteria stapedia.

The foramen ovale is differentiated from the foramen lacerum medium by a sinking of the nerve into the hind margin of the alisphenoid. In this way a shallow groove is formed which deepens into a notch and the notch is converted into a foramen by the junction of the margins of the notch behind the invading nerve. These transitions, resulting in the production of a complete foramen traversing the alisphenoid, have been effected independently in several mammalian phyla. The common statement that the foramen ovale "is at first a notch in the posterior border of the great wing of the sphenoid: it remains in this condition in all Mammals except Man"—is quite incorrect. Among the Primates the condition is very variable. In the lemurs, as in the Carnivora, it is a completed foramen situated some distance in from the posterior margin of the alisphenoid. In *Tarsius* it is absent, being simply represented in the general lacuna of the foramen lacerum medium. The condition of the foramen ovale as it is present in the Eocene lemur *Notharctus*, as well as in *Tupaia* and *Ptilocercus*, must surely make it difficult for the most enthusiastic supporter of the lemurine derivation of the higher Primates to picture the primitive haplorhine stage as developed from the specialised strepsirhine condition. In the Platyrrhini it may be present as a deep groove, a notch, or a practically complete foramen in the hinder margin of the alisphenoid. Among the Catarrhini it is usually represented by a notch in the alisphenoid completed behind by the anterior margin of the petrous, which may itself be reciprocally notched, to the lateral aspect of the tuba auditiva. In the orang and the chimpanzee it is situated at the posterior margin of the alisphenoid, being sometimes completed by that bone at its posterior aspect, but more commonly showing a posterior gap of variable size where the petrous is called upon to complete its periphery. In the gorilla its position and relations are altogether exceptional. Its oval axis is extended in an antero-posterior direction and it is situated on the lateral aspect of the hinder portion of the alisphenoid in which it forms a deep notch, its lateral aspect being completed by a corresponding notch in the squamosal.

In Man the foramen ovale may show a wide range of variations in respect to these features.

(*a*) It may be absent as a foramen by remaining confluent with the foramen lacerum medium, recalling the condition normal in the tarsiers and which may be described as tarsioid or primitive.

(*b*) It may be represented by any degree of completeness from a mere notch to an almost complete foramen encircled in over two thirds of its periphery by

the alisphenoid. This is the condition prevalent in most of the monkeys and anthropoid apes, and it may be termed pithecoid or incomplete.

(*c*) The gorilloid condition, in which the foramen is situated on the suture line between the lateral aspect of the alisphenoid and the squamous temporal, has not been recorded as occurring in Man.

From the pithecoid stage onwards to its completed condition the following definite stages may be met with in the human skull.

(*a*) The foramen may be situated wholly within the alisphenoid, but the route of ingress of the nerve into the bone may be marked by the presence of a suture passing through the posterior boundary of the foramen.

(*b*) The posterior bar may be completed, there may be no trace of a suture line, but the bar itself may be extremely slender, in some cases a mere spicule of bone separating the foramen ovale from the foramen lacerum.

(*c*) The posterior bar may be unduly broad, the foramen being thus situated unusually far in the substance of the alisphenoid. In its usual form the bar measures somewhat less than 6 mm. in a direction at right angles to its long axis.

(*d*) The foramen may be entirely cut off from the foramen lacerum, but it may communicate by a suture line or by a narrow chink with the foramen spinosum: or it may be variably confluent with this foramen. These variations are noted in connection with the foramen spinosum.

(*e*) It may be variably confluent at its anterior and medial extremities with the foramen of Vesalius.

(*f*) The foramen may vary widely in size and shape: most of these variations are dependent on the variations in the venous channels which find exit through it and they are noted in connection with these features.

(*g*) Asymmetry in size and shape between the foramina upon the two sides of the skull will usually be found to depend upon the same factors or to be correlated with asymmetry of the foramen of Vesalius.

(*h*) The anomalies that occur in connection with the subdivision of the foramen and the plane of its exit from the skull are, for the most part, dependent upon the disposition of the pterygoid processes and the pterygo-spinous bar.

(18) *The Foramen of Vesalius.* This foramen, in its classical form, is confined to Man and is essentially an expression of the differentiation of cranial venous outlets that is characteristic of *Homo*.

The foramen lacerum medium, like the foramen lacerum posterior, is the site of the egress of venous channels in the primitive Mammal, for the intracranial cavernous sinus conmunicates through this opening with the extracranial pterygoid venous plexus. With the subdivision of the foramen lacerum medium these venous channels are usually included with the nervus mandibularis in the foramen ovale. It is in fact the presence of these veins which, as a rule, in Man communicate inside the skull with Brechet's sinus and the cavernous sinus, that causes most of the typical variations in size and shape

of the human foramen ovale. The importance of the foramen ovale as a venous outlet from the human skull is a well-marked human distinction[1].

As a rule the veins tend to find their exit predominantly through the anterior and medial portion of the foramen, and the typical oval shape of the foramen is commonly due to this disposition of the veins in front and the nervus mandibularis behind.

(*a*) Occasionally the venous anterior portion of the foramen ovale is constricted and elongated and the whole foramen then assumes a pyriform instead of an oval shape.

(*b*) The venous portion of the foramen ovale may tend to become subdivided from the nervous portion by a narrowing of the orifice between the anterior and posterior compartments: this subdivision may proceed to the ingrowing of spicules of bone which may cut the foramen ovale into two parts, the anterior of which may be regarded as a foramen of Vesalius.

(*c*) In some cases the foramen of Vesalius obviously replaces the venous outlet of the foramen ovale, and then a small round foramen ovale is present in conjunction with a foramen of Vesalius lying some 2 or 3 mm. to its antero-medial aspect. This may be regarded as the maximum degree of subdivision of the foramen ovale.

(*d*) On one side, or on both, the venous outlet from the foramen ovale may be supplemented by an additional medial venous foramen—the foramen of Vesalius.

(*e*) When the foramen of Vesalius exists as a subsidiary venous channel it may assume a wide variety of forms.

(*f*) It may lie within 2 mm. of the antero-medial margin of the foramen ovale or it may be situated some distance forward in the fossa pterygoidea.

(*g*) It may exist as a single foramen, more or less oval in outline, or it may be present in the form of an elongated slit-like orifice.

(*h*) It may be represented by many orifices, irregular in size and shape, scattered over the interval between the foramen ovale and the pterygoid fossa.

(*i*) It may be present in some form or other on only one side of the skull: in such cases the size of the foramen ovale is usually notably different upon the two sides, being larger on that side on which the foramen of Vesalius is lacking. The foramen of Vesalius, as such, does not occur in any Primate other than Man.

(19) *The Foramen Spinosum.* The foramen spinosum, as a completed bony canal situated in the spina angularis of the sphenoid, is peculiar to Man. Its history is probably somewhat involved. The arteria meningea media, which alone gains ingress to the skull through its lumen, is almost certainly the representative of the superior (or supra-orbital) branch of the arteria stapedia "captured" by the external carotid. Originally arising from the stapedial artery after that vessel had emerged from the tympanum, the superior branch passed into the cranial cavity between the petrous and the alisphenoid to the lateral side of the nervus mandibularis with which it was associated. After

[1] See F. W.-J., *J. Anat. and Phys.* 1912, vol. XLVI, pp. 228–238.

the atrophy of the arteria stapedia this branch accompanying the mandibular nerve takes new origin from an anastomosis with the external carotid artery. The primitive point of entrance for the middle meningeal artery into the cranial cavity is, therefore, through the interspace between the alisphenoid and the petrous to the lateral side of the mandibular nerve. With the partial subdivision of the foramen lacerum medium the artery, like the mandibular nerve, tends to form its own bony canal, and in many members of several mammalian phyla the posterior margin of the angle of the sphenoid is notched for its reception. The condition in the Primates shows considerable variation.

In the tarsiers the initiation of an independent canal has not commenced. Among the Platyrrhines the artery passes through the foramen ovale in *Hapale* according to Beattie. In most of the Old World monkeys its point of entrance through the spheno-petrous fissure may be detected by the presence of a notch in the hind margin of the postero-external angle of the alisphenoid. In the anthropoid apes a very slight widening of the suture line and the occasional presence of a notch are the only evidences of its entrance into the cranial cavity and even these may be altogether wanting.

In Man, in its completed form, the foramen spinosum should properly be termed the canalis spinosus, since it is a passage of considerable length which tunnels the spina angularis to the lateral and posterior aspect of the foramen ovale. Nevertheless in Man it exhibits innumerable variations, all of which represent stages that, in some degree, fall short of its completed human form.

(*a*) It may be incompletely separated from the spheno-petrous interspace, being represented only by a deep and elongated incisura on the angular region of the alisphenoid. This condition may be termed pithecoid.

(*b*) It may be incompletely separated from the foramen ovale, a narrow isthmus connecting the two orifices.

(*c*) It may be complete at its cranial extremity, but incomplete below, in which case a gutter leads along the spina angularis to a foramen on the cranial floor.

(*d*) It may be complete below at the spina but incomplete above as it passes to the cranial cavity.

(*e*) It may be complete above and below but open over the intermediate part of its extent.

(*f*) It may communicate with the canaliculus innominatus which usually runs, in the form of a groove or of a minute canal, along its mesial margin.

(*g*) The foramen may perforate the apex of the spina angularis; it may be situated to the mesial aspect of the apex or even be some distance to the mesial aspect of the process itself.

(20) ***The Spina Angularis Sphenoidei.*** If we are to pay strict regard to the claims of priority in anatomical nomenclature, we should probably be justified in restricting the term "spinous process" or "spine of the sphenoid" to the backwardly directed postero-lateral prolongation of the alisphenoid inserted between the squamous and petrous portions of the temporal.

The variably developed process which depends from this postero-lateral angle of the alisphenoid should probably be rightly termed the "styliform process." The following quotations demonstrate the usage of these terms from 1726 to 1825:

(*a*) "The lowest and back part of each wing, which runs out sharp to meet the ossa petrosa, has been styled the spinous process; from near the point of which a sharp-pointed process is frequently produced downwards; which some call styliform" (Monro Primus, 1726).

(*b*) "The spinous process, which passing backwards dips down, and forms a little process, processus styliformis" (John Flint South, 1825).

In the first edition of Jones Quain's *Anatomy*, published in 1828 the terminology is somewhat altered:

(*c*) "The ala terminates posteriorly by a pointed prolongation, which is curved downwards, called the spinous process." By this terminology both the backwardly directed process and its dependent prominence are included in the term "spine of the sphenoid." This is not a desirable nomenclature since the dependent prominence is a very variable development occurring on the constant postero-lateral angle. If we are to adhere to the B.N.A. nomenclature it would be better to restrict the term spina angularis to the dependent prominence (or former styliform process) and employ the term processus angularis for the postero-lateral angle (or former spinous process). Restricting the term "spina" to the prominence developed upon the lower surface of the processus angularis we may say that in its complete human condition it may be defined by any of the generally accepted descriptive terms that have been applied to it. It has been termed "a sharp process" (Holden), "a prominent spine" (Morris, ed. 1), "a short sharp projection" (Quain, ed. 10), "a pointed process" (Gray, ed. 23), "une épine extrêmement saillante" (Poirier). Any such description must be restricted, however, to what we may term its ideal human condition: in a very great number of human skulls it does not arrive at anything approaching this stage of development. A processus angularis, in the sense that the postero-external angle of the alisphenoid is prolonged as a wedge between the squamous and petrous temporal, is a common mammalian possession: a spina angularis, in the sense of an independent spine of bone developed on the processus angularis, is a peculiar human development.

In the lemurs the processus angularis is prolonged backwards between the squama and the bulla: no spinous process is developed; and the prominence of the posterior extremity of the lateral lamina of the pterygoid passes *medial* to the region of the processus angularis. In the tarsiers the processus angularis is largely obscured by the bulla and it does not give rise to any spinous process. In the Platyrrhine the spine fails in its development and the posterior extremity of the lamina lateralis falls short of or passes *medial* to, the region of the processus angularis. In the Old World monkeys the condition differs fundamentally from that seen in the lemurs and New World monkeys, for the lamina lateralis of the pterygoid is prolonged to the apex of the processus angularis on

which it is present as a prominent ridge. This ridge passes *lateral* to the foramen ovale and it constitutes a complete pterygo-spinous bar—or lamina pterygo-spinosa. In the orang the processus angularis is reduced and the prominence of the lamina laterales either ends before reaching the angular area or else passes to it *medial* to the foramen ovale. There is no prominence that can properly be termed a spina angularis. In the chimpanzee the processus angularis is still more reduced and in the gorilla it is practically absent, being represented only by a spicule of bone posterior (not lateral) to the foramen ovale. In both the African anthropoids the lamina lateralis, if it has not become altogether lost at the posterior margin of the alisphenoid, passes *medial* to the foramen ovale. Although the processus angularis is thus reduced in the African anthropoids and the spina angularis cannot be said to exist, nevertheless there is, especially in the gorilla, an altogether peculiar bony prominence, at first sight simulating the spina angularis, but developed on the squamous temporal and not on the alisphenoid. This *spina angularis temporalis* is a gorilloid specialisation which has apparently been overlooked by those who have sought only for likenesses between *Homo* and the giant apes. Owen noted the general condition in the gorilla and emphasised the fact that the backward continuation of the lamina lateralis passed to the medial side of the foramen ovale. In his Memoir on the gorilla (1865, p. 20) he says: "the ridge which extends from the ectopterygoid along the inner border of the foramen ovale terminates in the Gorilla by an angle or process answering to that called 'styliform' or 'spinous' in Man, but of which there is no trace in the Chimpanzee, Orang or Gibbon." Owen, however, does not note that this process is a development of the temporal and *not* of the sphenoid.

In Man the condition of the spina angularis varies widely. It may take the classical form of being present as a prominent spine, developed from the processus angularis, or it may be hardly differentiated as an isolated elevation. It may be bifid, linear or serrated at its lower margin: and it may be, with varying degrees of completeness, connected with the lamina lateralis of the pterygoid process. It may be perforated by the foramen spinosum at its apex or upon its medial aspect, or it may be imperforate, the foramen entering the cranium some distance mesial to the spine.

(21) *Laminae pterygoidei.* The very widest range of variation exists in the Mammals generally concerning the development and disposition of the lateral and medial pterygoid processes. So wide is the range of variation that it is by no means always easy to homologise the underlying constituents with any degree of certainty. Fortunately these more rudimentary manifestations do not concern us here. The features of the greatest interest are displayed in the caudal continuation of the lamina lateralis and the relation of this extension to the foramen ovale.

In the lemurs the caudal extension of the lateral lamina passes medial to the foramen ovale and a perforation of the plate transmits part of the third division of the trigeminal towards the medial side.

In the typical pithecoid condition the pterygo-spinous bar is complete and it passes lateral to the foramen ovale, the perforation of the bar transmitting the nerve to the lateral side. In Man and the anthropoids the pterygo-spinous bar is usually not complete. When it is present in varying degrees of completion it gives rise to that group of anomalies in which the foramen of Civini and the porus crotopithecobuccinatorius of Hyrtl are included.

The range of variation of which note should be made in human racial studies may be classified as follows:

(*a*) The attached margin of the lateral lamina may fade away as a ridge upon the sphenoid anterior to the foramen ovale.

(*b*) It may pass back as a ridge to the anterior margin of the foramen and then this ridge may be distinctly to the mesial or to the lateral side of the foramen or it may be in the mid-point of the periphery of the anterior margin of the foramen.

(*c*) The ridge may pass back and effect some sort of continuity with the spina angularis sphenoidei and then the pterygo-spinous bar may pass laterally to the foramen ovale (pithecoid), medially (primitive) or even across the lumen of the foramen.

Apart altogether from this variation in the disposition of the caudal continuation of the lateral lamina great variations are shown in the degree of splaying of the two laminae and in their absolute and relative size. These features are of some racial significance.

(22) *The Jugular Fossa and Foramen.* Primitively, the exits of the internal jugular vein are of the same size upon the two sides of the skull. This equality is commonly present in the monkeys, but in the anthropoid apes disparity in size in favour of one side or the other is frequent. In the literature available I am unable to find any numerical statement as to the frequency of inequality in the anthropoids, or as to which foramen is most commonly the larger. Ward has given the results of an examination of 105 male white skulls and found equality in 12, a larger foramen on the left side in 15, and a larger foramen on the right in 78[1].

(23) *The Tympanic.* The fate of the tympanic in the lower Mammals needs no discussion since it is so amply dealt with in the literature. Its distinctions in the Strepsirhini have been frequently described and discussed. In the Haplorhini, the basal differences between the Platyrrhines and Catarrhines are well known; but its human distinctions and especially its human racial variations are not so completely recorded. The typical catarrhine pithecoid condition is for the tympanic external auditory meatus to take the form of an elongated tube which is comparatively smoothly rounded on all its aspects. In the gorilla alone is there developed any inception of that roughening of the lower surface that culminates in Man in the production of the roughened linear prolongation for the attachment of the perivascular fascial sheaths which is somewhat insufficiently named as the vagina processus styloidei. The development

[1] Ward, F. C., *Outlines of Human Osteology*, 1876.

of this rough ridge varies greatly in the human skull, and its massiveness in various portions of its length produces several different conditions. The ridge may fade away at its medial extremity, or it may constitute a sharp bony process that becomes practically continuous with the spina angularis sphenoidei. The development may be unduly slight in that portion which alone properly constitutes a vagina processus styloidei and then the styloid process fails to be an integral part of the skull: this being a primitive condition. It may be more than usually thin where it forms the floor of the external auditory meatus and the consequence may be the development, in some degree or other, of the foramen of Huschke, an anomaly that is very variably developed in different racial types. It may be unduly massive or unduly thin at the external auditory meatus: in the one case forming a thick bony mass surrounding the lower aspect of the meatus; in the other being present merely as a linear edge of a thin bony wall of the tube.

No account is here taken of exostoses developed within the external auditory meatus since the factors that lead to their development are not well understood. Whatever may be their causation, their racial incidence is very variable.

(24) *The Foramen of Huschke.* This is recorded by presence or absence on one or both sides; and by noting the foramen as large when its greatest diameter exceeds 5 mm.

(25) *The Styloid Process.* The fusion of the styloid process to the skull by its envelopment in the vagina processus styloidei is a human characteristic. This process of fusion may fail in the human skull, when the styloid processes are reported as absent. When the processes are present they may be well developed or small or be represented by the merest rudiments.

(26) *The Posterior Condyloid Foramen* is a distinctive human possession and its development in different racial types of skull is subject to the widest variation. The fossa condyloidea is a development independent of the canalis condyloideus: there may be a well-developed fossa but no sign of its perforation by the canal. These things are therefore recorded independently.

THE DATES OF UNION OF SOME EPIPHYSES IN EGYPTIANS FROM X-RAY PHOTOGRAPHS

By GIRGIS SIDHOM and D. E. DERRY

This investigation was originally undertaken with a view to ascertaining whether the commonly accepted idea as to the earlier maturity of Egyptians as compared with Europeans, generally, found any support in a possible earlier union of the epiphyses. At the same time an accurate knowledge of the most probable date of union of an epiphysis is of value in some medico-legal cases where the age of the person must be known, and where, as may still happen in Egypt, the date of birth is unknown. At the outset we were met with the difficulty that the dates of union of the epiphyses as given in the text-books exhibit such wide variation that the possibility of the comparison with Europeans at which we were aiming seemed likely to be defeated. Recently, however, two papers have appeared in this *Journal* (Davies and Parsons, Oct. 1927 and Paterson, Oct. 1929) in which an examination of X-ray photographs of epiphyses in persons of known age has been undertaken by these observers for English people, and a third paper by Dr L. Borovansky and Dr O. Hněvkovsky, published in *Anthropologie*, Prague, VII, 1929, gives amongst other observations on the growth of the body, the results obtained by X-ray examination of the epiphyses in boys of 4 years to 19 years of age in Prague, so that we have comparative figures for two European races.

At first sight it seems obvious that the only means of obtaining anything approaching accuracy in our knowledge regarding epiphyseal union is by X-ray examination, but as we shall see later this method of investigation is by no means free from error, for the question of how far union of an epiphysis with the shaft has proceeded is to a large extent dependent on the opinion of the observer in his interpretation of the X-ray film, and this allows of very wide differences in the recorded results. To lessen this source of error and to provide something in the nature of a definite point of departure in describing the appearances seen in the photograph, we have instituted a method of classification by stages, based on the known mode of ossification of the ends of long bones. While the shaft and its epiphysis are still widely separated by cartilage the difficulty does not arise, but as the cartilaginous interval lessens and bony union commences, the extent to which this has attained is often open to question and renders description of the state of union ambiguous, permitting therefore of widely differing dates being recorded for the union of the epiphysis and shaft. We believe that the method we have adopted lessens the liability to error, though it by no means obviates it entirely, but it does enable the results obtained by different observers to be more fairly compared. We divide the whole process into three stages.

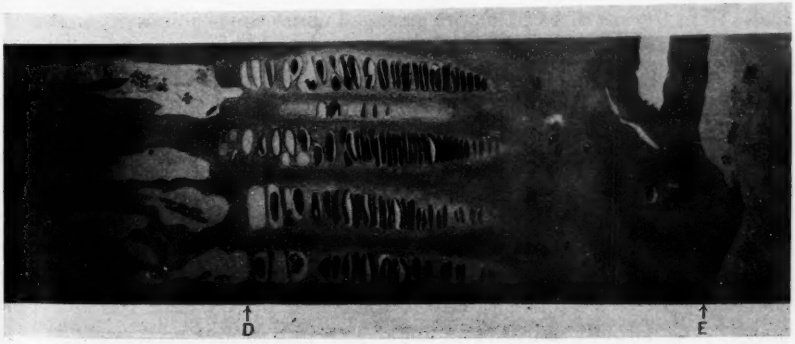
FIRST STAGE

(Plate I, fig. 1)

At this stage cartilage occupies the interval between the epiphysis and diaphysis and in the photograph the separation of the two is easily seen. If a section through these three parts is examined it is found that the cartilage is continuous with, or attached to, a relatively smooth and very thin plate of bone both on its diaphyseal as well as on its epiphyseal surface. These plates are well seen in any young macerated bone and present a very characteristic appearance (text-fig. 1).

Text-fig. 1. Upper end of radius with its epiphysis, showing the thin plate of bone on each, to which the cartilage is attached.

All the activities of bone formation and absorption take place in association with these bony plates, but are more marked in relation to the diaphyseal plate than to that of the epiphysis. The cartilaginous cells are arranged in rows and increase in size towards the diaphyseal plate (text-fig. 2), while in the region



Text-fig. 2. Section through growing end of young bone. *D* and *E* mark the sites of attachment of the cartilage to the diaphysis and epiphysis respectively. Note greater growth activity at diaphyseal attachment of cartilage.

of the epiphyseal plate they are fewer and scattered irregularly. In other words growth activity is most marked at the diaphyseal attachment of the cartilage, and while calcification and deposition of bone is proceeding on the cartilaginous side of the diaphyseal plate, on its opposite surface it is being absorbed continually and its place taken by cancellous bone.

Thus growth in length is taking place while the bony plate remains of the same thickness. A similar process occurs at the epiphyseal plate but is much less pronounced (text-fig. 2). As the bone approaches its full size the cartilage becomes thinner until the diaphyseal and epiphyseal plates eventually fuse and growth ceases. This terminates the first stage.

SECOND STAGE

(Plate I, fig. 2)

In this phase the plate of bone representing the fusion of the diaphyseal and epiphyseal plates is conspicuous and can be seen in the photograph as a dark line at the base of the proximal row of phalanges and also at the base of the 1st metacarpal bone.

THIRD STAGE

(Plate I, fig. 3)

This stage is reached when the bony plate is entirely absorbed and replaced by spongy bone (cf. Plate I, fig. 2). This may take months or even years and in a few cases it is still apparent in sections through bones of persons of advanced age.

These stages, or at least the first and second, allow of a more accurate classification of the age of a given bone from the state of growth of its epiphyses than has been the case in the past.

In the following tables the results of the examination by X-ray photographs of the upper extremity, excluding the shoulder joint, of over 400 Egyptian males from the age of 14 to 20, are arranged under the headings of the stages described above. Under First Stage are grouped "Entirely separate" and "Partially united" epiphyses, while the column "United" represents the second stage in which the plate of bone between epiphysis and shaft is still visible, plus the third stage in those cases where it has already been absorbed. With regard to the column headed "Partially united," it is almost certain that had opportunity permitted of a further examination within the year group the epiphyses in many of these individuals would have been found completely united, in which case the numbers in the column "United" would be increased with a corresponding rise in the percentage of united cases in any given year. But we have thought it better to adhere strictly to the stages already described although many of the partially united cases might with justice have been placed in the "United" column.

A source of uncertainty in regard to the dates of union as given by the various observers whose papers we have mentioned above is found in the some-

what loose way in which these dates are stated. We are told that an epiphysis remains separate "up to the 20th year." This *should* mean that it joins about the age of 19 or 19 and some months, but later we find it recorded as joining at 20 which in strict English is the 21st year. We do not wish to seem to be splitting hairs, but as we are concerned here with a comparison of the time of union of an epiphysis in two or more races, the difference of a whole year in the mean of a sufficiently large number of observations is significant, and for this reason, and in order that there may be no doubt whatever as to what is meant, we have grouped our results in years. For example "15–16" means that every case within that group had reached the age of 15 but had not passed 16. So soon as a person reaches 16 he is placed in the group 16–17 and so on. Of course this still allows of a possible discrepancy of nearly a whole year, some of the cases in the group having joined perhaps early in the group year and others near its end, but at least this arrangement allows of no ambiguity in description and it is hoped that as larger numbers are obtained it may be possible to cut the year groups into two of 6 months each. Further, the bald statement that a given epiphysis joins the shaft at 21 or 18–21 is not sufficient. It is important to know the most likely date of union in each case and in our tables this can be clearly seen. For example in Table II, giving the dates of union of the medial epicondyle, only 5·9 per cent. had united by the time the boys had reached 15. Between 15 and 16, nearly 20 per cent. are added making 25·6 per cent. united in the year group, while between 16 and 17 nearly 33 per cent. are further added so that at 17 years of age 58·1 per cent. are completely united. In the year group 17–18 another 26 per cent. join making 84·2 per cent. completely united by the time the boy reaches 18 years of age. Evidently from 16–18 are the years of most rapid growth and of these the group year 16–17 is the most fruitful for this particular epiphysis.

The subjoined tables explain themselves but we have added others exhibiting in a graphic form the percentages of all completely united epiphyses in the different year groups. These show the comparative state of union of all the epiphyses in relation to each other in a given year. Thus in Table XIII, which shows all the epiphyses of the upper limb which we have examined between the ages of 15 and 16, 62·5 per cent. have the epiphysis of the terminal phalanx of the thumb completely united, while the lower end of the radius is not completely united in a single case. In Table XIV, between the ages of 16 and 17, 8 per cent. have now reached complete union of the distal epiphysis of the radius, while over 84 per cent. of terminal phalanges of the thumb are completely joined. The early union of the terminal phalanx of the thumb does not seem to have been observed hitherto and should be of importance in medico-legal cases where the question of age has to be decided in young people.

We shall now attempt to compare our results for Egyptians with those of the observers above-mentioned.

THE DISTAL END OF HUMERUS

(Table I)

In Egyptian males the distal end of the humerus, excluding the medial epicondyle, is completely joined in 92·6 per cent. of cases by the time the subject has reached 17 years of age. Here we are in agreement apparently with Davies and Parsons who simply state in their list that it joins at 17. But in regard to the *earliest* union of this conjoined epiphysis (capitellum, trochlea and lateral epicondyle) with the shaft of the humerus there is a wide difference as between English and Egyptians, the former according to these observers not exhibiting union before 16 years 4 months, whereas in Egyptians, as can be seen in Table I, 35 per cent. of boys between 14 and 15 show complete union of the distal epiphysis with the shaft of the humerus. The discrepancy is even wider when we compare our results with those of Paterson who states that the epiphysis composed of the capitellum and trochlea joins the shaft "during the 19th year in males." If he means 19 years of age as appears to be the case from his list in Appendix II, then the Egyptian is some two years in advance of the English in the union of this epiphysis (see Table I). The results obtained on the other hand by Borovansky and Hnèvkovsky on Prague boys seem to agree with ours much more closely. On p. 193 of their paper (*cit. supra*) they say "The first fusion appears at 14 years of age. It is accomplished in most cases at 17, and always at 18 years of age." Here they are referring specially to the capitellum, but further on they remark in connection with the trochlea that its "fusion with the eminentia capitata and with the epicondylus lateralis begins in the 14th year, and it is accomplished in 75 per cent. of our cases, at 17 years of age." They add, "The epicondylus medialis fuses a year later." Their meaning is not very clear but their reference to fusion of the medial epicondyle seems to suggest that they are speaking not only of fusion of the different parts of the lower end of the humerus with each other, but also to the shaft, and if this is what they intend to convey, it more nearly agrees as already remarked with our results, although in Egyptian boys of between 15 and 16, 76·7 per cent. exhibit complete union, which therefore is an advance of at least a year on the Prague boys (75 per cent. at 17 years of age, see above).

THE MEDIAL EPICONDYLE

(Table II)

The date of union of this epiphysis has been generally recognised to be later than that of the rest of the lower end of the humerus. Our observations confirm this to the extent that only 58·1 per cent. of medial epicondyles are found fully united in the group year 16–17, whereas in the same year 92·6 per cent. of the cases examined show the distal epiphysis of the humerus completely joined. Davies and Parsons say, "The internal epicondyle remains separate up to the 20th year except for one observation at 18 years 2 months, when it was distinctly joined. It is an open matter whether this epicondyle joins the

shaft before or after the head of the humerus." This is not our experience, as may be seen from Table II, where 84 per cent. are joined by the time the boys have reached 18. We may add, further, in regard to the last sentence of the quotation we have just given, that it is quite certain that the head of the humerus joins later than the medial epicondyle as we possess numerous examples of actual skeletons in which the medial epicondyle is completely fused while there is no sign whatever of even commencing union in the epiphysis of the head.

Paterson finds that the medial epicondyle joins the shaft "somewhere between eighteen and twenty-one in males." Here again we would draw attention to the value of our year groups, where it is seen that while a small number of Egyptians still exhibit lack of complete union in the year group 19–20, 95·8 per cent. have already joined by that date, and only 4·6 per cent. have been added since the previous year by which time 91·2 per cent. were united. Borovansky and Hnèvkovsky are again more closely in agreement with us. They say, "The centre in the epicondylus medialis begins to fuse at 14 years of age, and the fusion is accomplished in 67 per cent. of all cases at 17, and in 95 per cent. of all cases at 19 years of age." These results are practically the same as those given in our Table II, our earliest case of union being at 14 years 1 month, and our latest ununited at 19 years 3 months and this was partially united.

PROXIMAL END OF RADIUS

(Table III)

In the case of this epiphysis Davies and Parsons "put the average age of junction as the 15th to the 16th years." This is presumably equivalent to our year groups from 15–17, during which period there is an increase of 56 per cent. over the number of united cases *before* 15 years of age. But 24 per cent. are still added in the group year 17–18 and thereafter the number drops very suddenly. Our centre point is therefore round about the age of 16. Paterson says of this epiphysis, "It joins the shaft very constantly during the 18th and 19th year." As our table shows, 88·3 per cent. of our cases are already united by the age of 18 and the latest age with epiphysis still separate is 18 years 6 months. By 19 years of age every one is joined. Borovansky and Hnèvkovsky state that fusion with the diaphysis begins after 14 years of age and is accomplished in the 18th year, "when in most cases not even the structure shows any trace of the epiphyseal line." This again is in close agreement with our observations. See note in Table III in reference to absorption of the bony plate.

It is difficult in this case to say how much earlier the Egyptians are than the English. We are inclined to think that they are in advance on the average, but a fair comparison is impossible owing to the manner in which the results of observations on the latter race are presented.

DISTAL END OF RADIUS
(Table IV)

This epiphysis is the latest to join in the upper limb with the exception of the upper end of the humerus which is not included in our investigation. In 99 cases examined in the group year 16–17, only 8 per cent. were completely united. This percentage is doubled in the following group year 17–18, but the largest number are found to unite between 18 and 19. Davies and Parsons give the 19th–20th year as the commonest time of union in England. We interpret this as meaning 19–20 as indeed it is so stated in their summary. Paterson says, "In males it was not found to have joined the shaft constantly until the twenty-first year, only in 50 per cent. of cases had it joined at twenty." It will be seen by reference to Table IV that 69·6 per cent. of our cases were completely united by the time the subject had reached 20, and 48·6 per cent. were united in the group year 18–19, so that so far as the observations go the Egyptians are at least a year ahead of the English in this regard. Borovansky and Hnèvkovsky say, "fusion of the epiphysis with the diaphysis begins in isolated cases in the 16th year, at 18 years of age the epiphyseal lines can be distinguished—at 19 years of age the process is accomplished." The reference here to epiphyseal lines probably means what we term the bony plates which, owing to the disappearance of all cartilage, are now in contact and show as a dark line in the X-ray photograph (see Plate I, fig. 2, bases of phalanges). If this is so it corresponds to our Second Stage when the epiphysis and shaft are united, and as these observers give 18 years for this it would correspond to our group year 18–19, when the largest number become united.

DISTAL END OF ULNA
(Table V)

This epiphysis joins the shaft a little earlier than that of the radius. It was first noticed as completely united in the group year 15–16, where one case in 41 was joined. In the group year 16–17, 9·5 per cent. are united, and from 17–18 and again from 18–19 there is very active growth, nearly 43 per cent. being added in the two years, so that by the time the boys reach 19, 52·2 per cent. are completely joined. Davies and Parsons give 20 as the date of union, Paterson 21, who also says that it joins at the same time as the radius, but we find it almost constantly ahead (see Tables XIII–XVII).

Borovansky and Hnèvkovsky also state that "the epiphyseal zone of the ulna disappears simultaneously with the epiphyseal zone of the radius." As just stated this is not our experience.

This epiphysis like that of the radius appears therefore to join earlier on the average in Egyptians than in the English.

FIRST METACARPAL
(Table VI)

In none of the epiphyses which we have dealt with above is the divergence from what is described by the observers we have quoted so wide as in the 1st metacarpal bone. Davies and Parsons found only two out of eight cases (25 per cent.) joined in the 17th year. As their 17th year is our 17–18 group the difference is remarkable as it can be seen from our table that 89·6 per cent. are completely united in this year. They add further that "in all observations in the 18th year it has joined and remains so from thence onwards except for one case of 22 years when it was still complete and separate." Such a rapid change from 17 to 18 is quite unlike anything in our experience where, as can be seen in Table VI, there is a steady increase in the number of united cases up to 18, when 89·6 per cent. are found to be joined, and thereafter in the year group 18–19 a further small percentage is added. Paterson groups his results for this epiphysis with those of the other metacarpals, but the differences as compared with ours are even wider. At 16 years (our 16–17 year group) he finds only 4 per cent. of united cases, as compared with 20 per cent. (1 in 5) in Davies and Parsons, and 68·3 per cent. in ours.

SECOND TO FIFTH METACARPALS
(Table VII)

What has been said for the 1st metacarpal applies generally for the epiphyses of the 2nd–5th except that the latter appear to be slightly behind the first. Davies and Parsons quote observations on Dartmouth Cadets in whom no union had occurred in the 17th year. Taking this to mean our year group 17–18 we have 83·3 per cent. fully united, and even up to the age of 17 we find 63 per cent. completely joined. If our observations are correct the Egyptians are far in advance of English males.

THE PHALANGES
(Tables VIII–XI)

According to our observations the epiphyses of the distal row are the first to unite and the terminal phalanx of the thumb is the earliest of all. In the year group 14–15 out of 102 cases examined 16 had the ungual phalanx of the thumb completely united. None of the observers we have quoted appears to have noticed this. Davies and Parsons observed that the earliest phalangeal epiphyses to unite were those of the distal row and their earliest case was at 16 years 9 months. It will be seen from Table X that in the corresponding period, year group 16–17, 72 per cent. of Egyptians have the epiphyses of the terminal row, 2nd–5th, completely united, while at the same age 84·3 per cent. have the epiphyses of the ungual phalanx of the thumb fused (Table XI). Borovansky and Hnèvkovsky say that fusion of the phalangeal epiphyses

begins in the 14th year, first in the basal phalanges, but add that in the terminal phalanges the epiphyseal lines disappear sometimes earlier than in the middle phalanges. They found that the epiphyseal lines had entirely disappeared in all the phalanges in 30 per cent. of boys aged 16. Our percentages at the same age are 72 for the terminal row, 60 for the first row and 57·7 for the middle row, and as will be seen from the tables, the Egyptians have reached 30 per cent. a year earlier than seems to be the case in the Prague boys.

CONCLUSIONS

From the results obtained and classified in the accompanying tables, we believe we have evidence that Egyptian males are definitely earlier than English in the union of some at least of the epiphyses of the upper limb. At the same time the wide divergence in results as between ourselves and the observers we have quoted as well as between those observers themselves seems to illustrate the unreliability of results obtained even from X-ray photographs. That such a statement as that quoted above from Davies and Parsons should be possible, viz.: "that it is an open matter whether the medial epicondyle joins the shaft before or after the head of the humerus" throws the gravest doubt on the value of opinions derived from examination of X-ray films of at least some uniting epiphyses. This is especially true of those epiphyses which fit in a cap-like fashion over the top of the shaft as in the case of the epiphysis of the humeral head and the heads of the metacarpal bones. It renders investigation of the extent of union of the epiphysis of the iliac crest practically valueless as one of us (D.E.D.) found after a series of X-ray photographs of this region had been taken. Owing to the convexity of the iliac crest, over which the uniting and deeply concave epiphysis fits very closely, all signs of a gap which to the naked eye is obvious are obliterated in the photograph. This was proved, after suspicions had arisen in the mind of the investigator, by photographing the hip bone of a young subject in which the epiphysis of the crest was only partially united, leaving a large gap which had been occupied by cartilage in the recent condition. An iron nail was inserted in the gap and the bone X-rayed and in the resulting picture the nail appeared to be fixed in solid bone, no trace whatever of the wide gap between the edge of the epiphysis and the crest over which it lay being visible in the photograph.

In view of the above facts we hold that the method we have adopted and described in this paper does at least limit the possibilities of wide discrepancy as between different observers, it being a comparatively easy matter to be sure when all cartilage has disappeared leaving the dark line representing the union of the diaphyseal and epiphyseal bony plates, our Second Stage.

We have a further advantage in that all our photographs were taken expressly for the purpose of this investigation and not selected from X-rays taken for a variety of reasons in a hospital. Every subject was treated in the same

way with the hand and arm in the same position, so that a much fairer comparison is possible than can otherwise be the case.

The value of grouping results so that the percentage of united cases in any year may be seen at a glance is brought out conspicuously in the comparisons we have made with those of the observers quoted throughout this paper.

Table I. *Distal end of humerus (excluding medial epicondyle)*

Age in years	Cases examined	First stage: Entirely separate	First stage: Partially united	2nd and 3rd stages united	% of fully united cases
14–15	91	51	8	32	35·16
15–16	43	10	0	33	76·74
16–17	95	4	3	88	92·63

Table II. *The medial epicondyle*

Age in years	Cases examined	First stage: Entirely separate	First stage: Partially united	2nd and 3rd stages united	% of fully united cases
14–15	101	94	1	6	5·94
15–16	39	24	5	10	25·64
16–17	98	37	4	57	58·16
17–18	95	11	4	80	84·21
18–19	68	6	0	62	91·17
19–20	24	0	1	23	95·83

Earliest ages of union

Case no.	Age Y.	M.	D.
542	14	1	3
597	14	3	24
558	14	7	8
578	14	8	20

Latest age with epiphysis still separate

Case no.	Age Y.	M.	D.
282	19	3	4

In this case the epiphysis was found partially united.

Table III. *The proximal end of radius*

Age in years	Cases examined	First stage: Entirely separate	First stage: Partially united	2nd and 3rd stages united	% of fully united cases
14–15	99	91	0	8	8·08
15–16	41	20	8	13	31·70
16–17	98	20	15	63	64·28
17–18	94	6	5	83	88·29
18–19	67	3	2	62	92·53
19–20	37	0	0	37	100

Earliest ages of union

Case no.	Age Y.	M.	D.
542	14	1	3
597	14	3	24
558	14	7	8
578	14	8	20

Latest ages with epiphyses still separate

Case no.	Age Y.	M.	D.
393	18	6	28
364	18	2	17
497	18	0	5

The earliest case which we had for the absorption of the bony plate was no. 578 at the age of 14 years 8 months 20 days, and by the 20th year it is very rare to meet a bony plate not fully absorbed.

Table IV. *The distal end of radius*

Age in years	Cases examined	First stage: Entirely separate	First stage: Partially united	2nd and 3rd stages united	% of fully united cases
14–15	104	104	0	0	0·00
15–16	41	38	3	0	0·00
16–17	99	81	10	8	8·08
17–18	90	44	30	16	17·77
18–19	70	22	14	34	48·57
19–20	23	2	5	16	69·56

The bony plate formed in the second stage of union takes from one to one and a half years to absorb.

Table V. *The distal end of ulna*

Age in years	Cases examined	First stage: Entirely separate	First stage: Partially united	2nd and 3rd stages united	% of fully united cases
14–15	104	104	0	0	0·00
15–16	41	32	8	1	2·43
16–17	94	52	33	9	9·46
17–18	87	15	46	26	29·88
18–19	69	8	25	36	52·17
19–20	24	0	6	18	75·00

Earliest ages of union

Case no.	Age Y.	M.	D.
271	15	11	2
178	16	4	3
285	16	4	22

Latest ages with epiphyses still separate

Case no.	Age Y.	M.	D.
498	19	8	28
482	19	4	13
234	19	3	25
282	19	3	4

This epiphysis does not show the bony plate when examined by the X-ray though it is actually present.

Table VI. *The first metacarpal bone*

Age in years	Cases examined	First stage: Entirely separate	First stage: Partially united	2nd and 3rd stages united	% of fully united cases
14–15	110	96	4	10	9·09
15–16	42	25	3	14	33·33
16–17	101	27	5	69	68·31
17–18	96	6	4	86	89·58
18–19	71	5	0	66	92·92
19–20	24	0	0	24	100

Earliest ages of union

Case no.	Age Y.	M.	D.
542	14	1	3
597	14	3	24
558	14	7	8
578	14	8	20

Latest ages with epiphyses still separate

Case no.	Age Y.	M.	D.
357	18	8	12
393	18	6	28
364	18	2	17
351	18	1	20

The bony plate formed in the Second Stage is absorbed somewhat later than that of the *proximal* end of radius. It has usually disappeared about the 19th year and it is very rare to find a plate at the age of 22 which is not fully absorbed.

Table VII. *Metacarpals from 2nd–5th*

Age in years	Cases examined	First stage: Entirely separate	First stage: Partially united	2nd and 3rd stages united	% of fully united cases
14–15	110	104	0	6	5·45
15–16	42	26	6	10	23·83
16–17	100	33	4	63	63·00
17–18	96	14	2	80	83·33
18–19	71	6	0	65	91·54
19–20	23	0	1	22	95·65

Earliest ages of union

Case no.	Age Y.	M.	D.
542	14	1	3
597	14	3	24
558	14	7	8
578	14	8	20

Latest ages with epiphyses still separate

Case no.	Age Y.	M.	D.
282	19	3	4
357	18	8	12
393	18	6	28

These epiphyses in their union show no bony plates when examined by X-ray though they are actually present.

Table VIII. *Phalanges proximal row*

Age in years	Cases examined	First stage: Entirely separate	First stage: Partially united	2nd and 3rd stages united	% of fully united cases
14–15	102	95	0	7	6·86
15–16	42	26	3	13	30·90
16–17	101	39	1	61	60·39
17–18	95	10	1	84	88·42
18–19	70	6	0	64	91·42
19–22	36	0	1	35	97·22

Earliest ages of union

Case no.	Age Y.	M.	D.
542	14	1	3
597	14	3	24
558	14	7	8
578	14	8	20

Latest ages with epiphyses still separate

Case no.	Age Y.	M.	D.
282	19	3	4
357	18	8	12

In case no. 282 the first and second were united but the remaining three phalanges were partially united.

The ages given above in the early united cases indicate the second stage of union, i.e. when the epiphyses are united by bony plates. These bony plates take from one to one and a half years to absorb.

Table IX. *Phalanges middle row*

Age in years	Cases examined	First stage: Entirely separate	First stage: Partially united	2nd and 3rd stages united	% of fully united cases
14–15	102	95	1	6	5·87
15–16	40	27	1	12	30·00
16–17	97	37	4	56	57·74
17–18	94	8	5	81	86·17
18–19	62	5	1	56	90·32

No bony plate appears on X-ray examination though it is actually present.

Table X. *Phalanges terminal row from 2nd–5th*

Age in years	Cases examined	First stage: Entirely separate	First stage: Partially united	2nd and 3rd stages united	% of fully united cases
14–15	107	96	1	10	9·34
15–16	39	25	0	14	35·89
16–17	94	26	0	68	72·34
17–18	89	6	3	80	89·88
18–19	70	4	1	65	92·85

The bony plate formed in the second stage of union is well developed and shows clearly in X-ray plates, and it takes about four years to absorb. It is interesting to note that the epiphyses of the terminal phalanges are the first to unite and the last to have their bony plates absorbed.

Table XI. *Terminal phalanx of thumb*

Age in years	Cases examined	First stage: Entirely separate	First stage: Partially united	2nd and 3rd stages united	% of fully united cases
14–15	102	81	5	16	15·68
15–16	40	11	4	25	62·50
16–17	95	15	0	80	84·27
17–18	90	1	8	81	90·00
18–19	70	3	0	67	95·71

Table XII. *Comparison between the percentages of completely united epiphyses in cases examined between the ages* 14 *to* 15

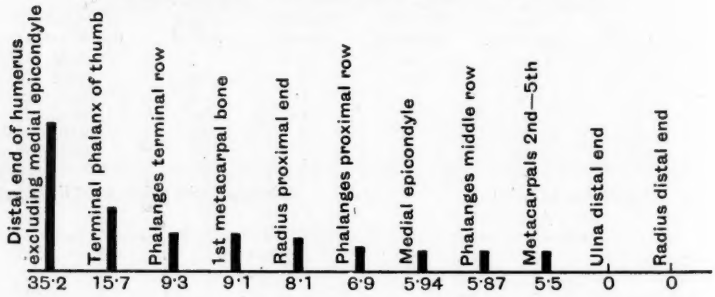


Table XIII. *Comparison between the percentages of completely united epiphyses in cases examined between the ages* 15 *to* 16

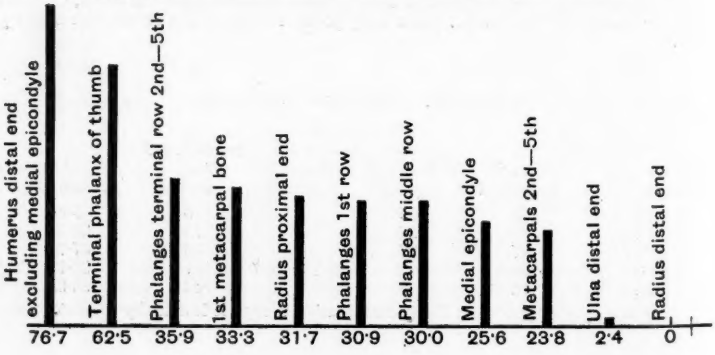


Table XIV. *Comparison between the percentages of completely united epiphyses in cases examined between the ages* 16 *to* 17

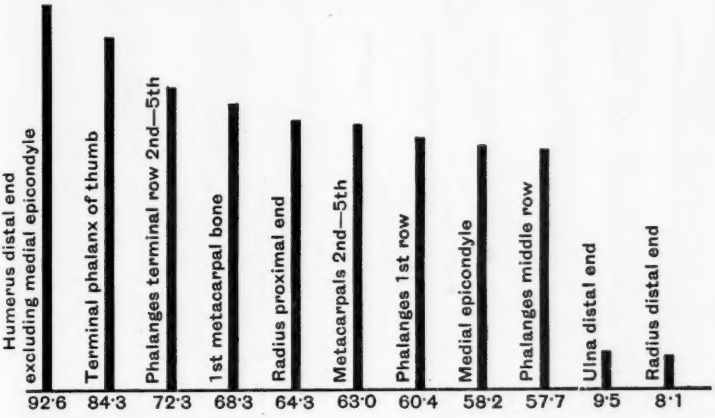


Table XV. *Comparison between the percentages of completely united epiphyses in cases examined between the ages* 17 *to* 18

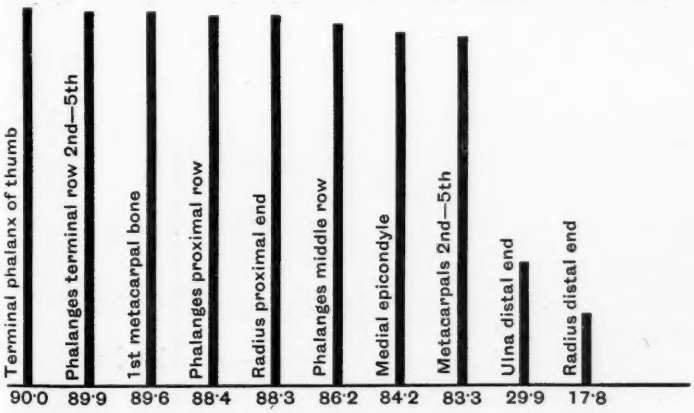


Table XVI. *Comparison between the percentages of completely united epiphyses in cases examined between the ages* 18 *to* 19

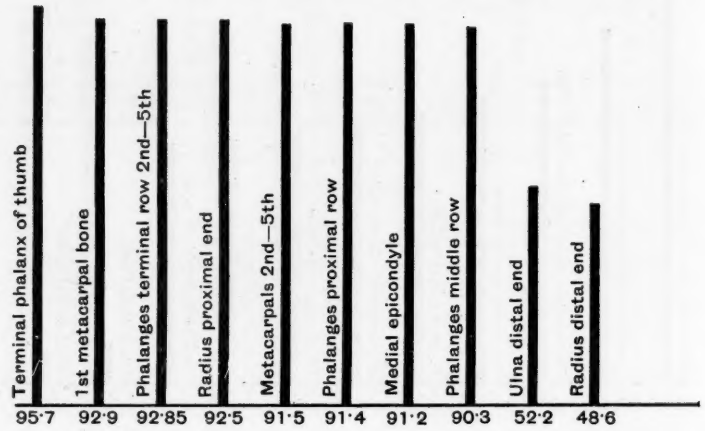


Table XVII. *Comparison between the percentages of the completely united epiphyses of the distal ends of both ulna and radius at different ages*

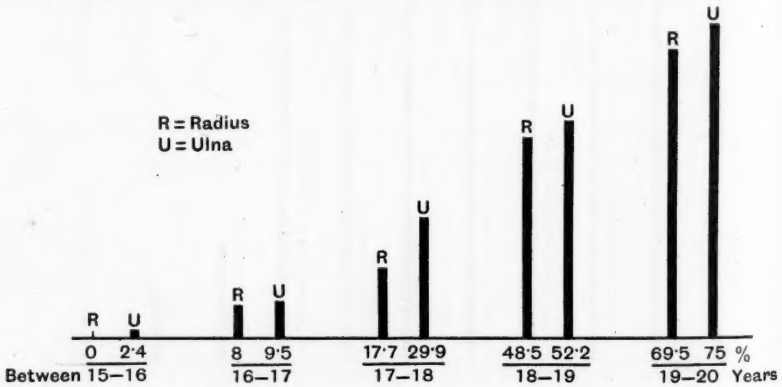


Fig. 1

Fig. 2

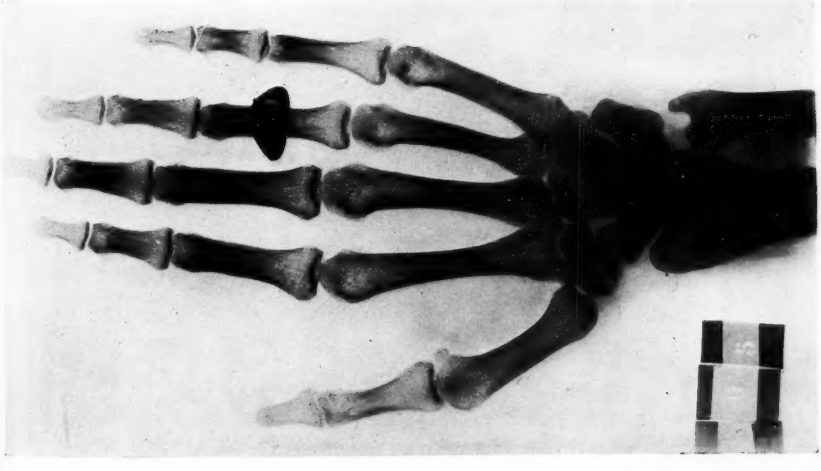


Fig. 3

UNIV. OF MICH.

(1)

(2)

(3)

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Fig.

Fig.

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EXPLANATION OF PLATE I

Fig. 1. Illustrating the first stage when the cartilaginous interval between diaphysis and epiphysis is conspicuous.

Fig. 2. Exhibits the second stage when the epiphysis is united and the bony plate appears as a dark line. This is seen in the bases of the proximal row of phalanges. In the distal row the line is disappearing, as the epiphyses have united somewhat earlier. The epiphyses of the middle row of phalanges are still ununited. The epiphysis at the base of the first metacarpal is also united and shows the bony plate of union.

Fig. 3. Third stage. The bony plates have been absorbed.

ATTEMPTS TO PROMOTE THE RE-FORMATION OF GERM CELLS

By MARGARET HILL
and A. S. PARKES (*Beit Memorial Research Fellow*)

From the Department of Physiology and Biochemistry, University College, London

I. INTRODUCTION

It has recently been supposed by a number of workers (1, 3, 4, 6) that oocytes may be formed after puberty from the germinal epithelium of the ovary of the normal female, and it has furthermore been suggested that cyclical neo-formation takes place corresponding to the oestrous cycle. In most cases, however, the critical prophase stage has not been observed in the adult, and in the absence of this stage some doubt exists as to the validity of the observations.

It seems certain, however, that oocytes may be re-formed in the adult animal after the complete excision of all tissue which may reasonably be called ovarian (see (7) for discussion), and there is thus nothing inherently impossible in the idea that the normal adult ovary may be capable of the neo-formation of germ cells. On the other hand, existing oocytes may be completely obliterated by exposure to X-rays, and under these conditions no new formation of germ cells takes place (2). In such experiments, however, it is necessary to remember the possibility of permanent damage having been done to the germinal epithelium by the X-irradiation.

In view of the general confusion of the problem of the neo-formation of oocytes, and especially because of the reported cyclical production, it was thought desirable to investigate the influence, if any, exerted by the anterior pituitary body on the re-formation of oocytes. Injection of the normal female seemed to be unpromising, because of the difficulty of assessing the relative number of oocytes present before and after treatment. Series of injections of preparations containing the gonad-stimulating principle of the anterior pituitary body have therefore been administered to:

(*a*) Ovariectomised mice showing no sign of ovarian regeneration.

(*b*) Mice exposed to a dose of X-rays known to be sufficient to eliminate all oocytes.

II. METHODS

Ovariectomy. The operations were carried out as before (7), except that the top of each uterine cornu was removed in addition to the fat body, Fallopian tube, capsule, hilum and ovary.

X-irradiation. Young mice 3–4 weeks old were exposed for 80 minutes to X-rays of the type and intensity used previously (2). Such dosage obliterates all oocytes and therefore in time all normal follicles, sterility becoming absolute in most mice in 4–6 weeks.

Extracts. The alkali extracts of ox anterior pituitary tissue were made by the method reported by Teel (8), while the tissue suspensions and urine extracts have previously been described (5).

III. EXPERIMENTAL RESULTS

Ovariectomised mice. Eleven mice, 2 months after ovariectomy, were injected over a period of 5–9 weeks with urine extracts containing the gonad-stimulating principle of the anterior pituitary body. Five mice received five and six mice received three series of injections, each series consisting of an injection per day for 1 week, 1 week's interval being allowed between each series. Of the eleven mice, only one showed signs of spontaneous cornification of the vagina (indicating re-formation of ovarian tissue) after the treatment. This proportion is no greater than that found in un-injected ovariectomised mice (7). It may be concluded, therefore, that administration of anterior pituitary hormone after ovariectomy does not facilitate the regeneration of ovarian tissue, which may sometimes occur after complete double ovariectomy.

Irradiated mice. Twenty irradiated mice were injected with extracts containing the anterior pituitary hormones. The details are given in Table I.

Table I

Type of extract	No. of animals	Days injected	Time of autopsy after last injection (days)	Result
Alkali extract of ox anterior pituitary	12	9–15	1–5	No oocytes present
Suspensions of mouse pituitary	6	5–7	1–10	,,
Urine extract	2	Two series of 7 daily injections with 3 weeks' interval	3	,,

No oocytes whatever were found in these animals, and it is evident that such treatment will not restore to irradiated animals the capacity to produce oocytes. The small anovular follicles appearing in the second post-irradiation proliferation from the germinal epithelium in irradiated mice (2) were very plentiful in the injected animals, but it is difficult to say if their production was increased.

IV. SUMMARY

The administration of preparations containing the gonad-stimulating principle of the anterior pituitary body does not (*a*) increase the percentage of ovarian regeneration in ovariectomised mice, or (*b*) cause the re-formation of oocytes in mice sterilised by exposure to X-rays.

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THE INNERVATION OF THE OCULAR MUSCLES

By H. H. WOOLLARD
Anatomy Department, St Bartholomew's Hospital Medical College

In a communication to the Anatomical Society made in 1926 a description of the nerve fibres and endings found in the ocular muscles was given. It was stated that there were present two kinds of nerve fibres, thick and thin. The former were of the ordinary medullated kind and terminated in hypolemmal muscle plates in the usual manner. The thin fibres were either very finely medullated or entirely non-medullated. They bore several endings, sometimes complicated and sometimes simple; they might be epilemmal or hypolemmal; several might occur on one muscle fibre, and the particular muscle fibre receiving this kind of innervation appeared to be thinner than the muscle fibre receiving the more usual motor terminal plate.

The problem arising out of these observations concerns not so much the morphological aspect, for there is agreement among many observers (Retzius, Dogiel, Huber, Boeke, etc.) that such fibres do occur, but rather the interpretation of them. Huber, Dogiel, Sherrington and Tozer believed that the thin fibres were sensory, while Boeke, both on morphological grounds and as the result of experiment, concluded that they ultimately belong to the sympathetic nervous system coming from the superior cervical ganglion.

MORPHOLOGICAL OBSERVATIONS

A great deal of material from animals, such as the cat, dog and rabbit, has been studied at various times as well as sections from human ocular muscles. Ocular muscles were obtained from a post-mortem on a woman who had been dead twenty-four hours. The material was stained by the Bielschowsky method and the following observations were recorded. Nerve bundles were stained abundantly and could be observed both in longitudinal and transverse section. In a bundle cut longitudinally eight nerve fibres were present. Of these six were large and thick, while two were of the finer kind. When bundles cut in cross section were examined it was not possible to identify any fine fibres. All the nerves appeared to be of the same size. In all cases examined the axis cylinder was clearly stained. The medulla was of a granular opaque appearance and the neurilemma jet black. When the fibres contained in any bundle were separating out in order to advance to their particular terminations it was then possible to distinguish readily both coarse and finer fibres. The coarser fibres showed numerous moniliform thickenings which are presumed to be the result of post-mortem changes. Many fine fibres can also be now distinguished. These are seen running about the muscle fibres but the method used did not permit

a detailed observation of the manner in which they ended. Nevertheless they seemed to be quite independent of the coarser system of the fibres.

Some other observations are recorded because they have been made by Tiegs the basis of a theory, with some points of novelty, of muscle action and the relation of nerves to muscle fibres. Silver preparations afford a valuable means for studying fibrous and reticular tissue and also bring out the sarcomeres of the muscle fibres with clearness. Tiegs has stated that Krause's membrane forms a continuous spiral. This appearance certainly occurs but is visible not only at the periphery of the muscle fibre but also in the substance of the muscle fibre. It is due to the dark appearance of the longitudinal bands. These shift in position as the focus is varied and this is the explanation of the apparent continuity of the Krause membranes.

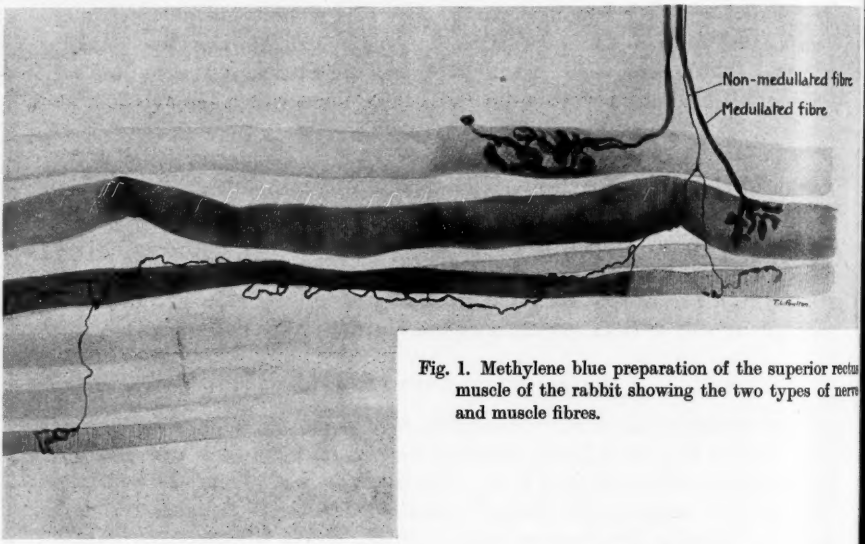

Fig. 1. Methylene blue preparation of the superior rectus muscle of the rabbit showing the two types of nerve and muscle fibres.

Tiegs also suggested that nerve fibres form a series of fine fibrillae which become continuous with the spiral membrane of Krause. In these preparations strands are present which appear to connect with Krause's membranes. As a matter of fact on careful focussing these strands certainly only come into contact with the surface of the muscle fibre, and they are fibrous and not nervous.

The membranes of Krause can be followed right to the sarcolemma, and where the sarcolemma is elevated by the presence of a nucleus of the muscle fibre the membrane can be traced across the nucleus right to the sarcolemma.

In the study of material from various animals the clearest and most notable results have been obtained by the use of the methylene blue intra-

vitam method of staining. The mode of innervation already described has been seen in the cat, dog, rabbit and rat. These animals, along with those investigated by other workers, makes it extremely probable that the same description would apply to all Mammals including Man.

There is some reason to suppose that a similar kind of innervation obtains in the tongue, perhaps also in the muscles of the face and in the muscles of mastication, but this statement needs further investigation before it can be accepted.

My own investigations and those of numerous other observers (Wilkinson most recently for instance) make it quite certain that the mode of innervation of the ocular muscles does not occur in the somatic musculature of the trunk or limbs. It is peculiar to a restricted region of muscles, even if not actually to the eye muscles themselves. At the moment there seem to be established for eye muscles three distinguishing features, the first being the peculiar type of innervation which we have been discussing.

Secondly, there is the reaction to acetyl choline. It has been known for a long time under the name of Vulpian's phenomenon that a sustained contraction could be got from the tongue muscles, though the hypoglossal had been previously severed, by stimulating the chorda tympani. A fresh interest has been given to this observation by the recent discovery of Dale that striate muscle when denervated and perfused with fluid containing acetyl choline behaves in a similar manner. The investigations of Duke-Elder have led him to declare that the eye muscles are the only muscles in the body which give a prolonged tonic contraction to acetyl choline without previous denervation.

And finally one cannot help drawing attention to the very significant rôle that eye movements play in all our visual judgments.

Huber regarded these fine fibres with their endings as being the sensory nerves of the ocular muscles. He supported this opinion with the following reasons. Since the ordinary type of ending is already present in these muscles it is obviously logical to infer that a second and different type would belong to the sensory side. He emphasised the epilemmal situation of their endings. This, however, needs some qualification. For the most part they are certainly epilemmal, but in some instances they also appear to be hypolemmal. He urges the fact that more than one of these endings is to be found on the same muscle fibre. This indeed supports his argument as does also his observation that no other kind of ending is present that can be associated with a sensory function. Dogiel and Sherrington concur in this interpretation, but it leaves unaccounted for the fact that these endings differ, not only in their form, but also in the type of fibre that carries them, very considerably from the usual medullated fibre and neuro-muscular spindle.

In the communication already referred to I compared these observations with those of Boeke. He believes these fibres to be of sympathetic origin and brings their distribution into accord with his conception of the double innervation of each individual muscle fibre. This I suggested could not be so, for if

these fibres were of sympathetic origin then they followed a distribution which gave to one muscle fibre a typical motor ending and to a different fibre a second type of ending—a conception used by Hunter and Royle.

It has long been known and was again brought into prominence by Kulchitsky that the striate muscle of cold-blooded animals exhibits a kind of innervation that resembles very closely, even if it is not identical with, that of the ocular muscles in Mammals. In addition to the ordinary motor terminal plates of medullated nerves a series of fine fibres are also present forming both epilemmal and hypolemmal endings. No ready explanation can be found to suggest why such a delicate and finely poised mechanism as the ocular muscles rather than other muscle groups in the Mammals should retain a closer morphological resemblance in their innervation to what happens in all the striate muscles of cold-blooded vertebrates. If the second finely medullated system does persist in Mammals, one must find a reason why its hypolemmal and presumably motor portion has disappeared, and only its afferent side is retained. Wilkinson accepts the sensory rôle of this system in the ocular muscles and looks on them as a reserve kind of innervation possessing an embryonic character and capable of further development. For this idea there appears to me to be not the slightest evidence. Moreover it seems very anonalous that an arrangement repeating the type found in the lower Vertebrates and therefore to be regarded as less efficient functionally should appear only in the eye muscles, where there is the best of reasons for expecting to find the most perfect proprioceptive system in the body.

THE SIZE OF THE MUSCLE FIBRES

It has been suggested that this special fine type of innervation is related not only to the tendinous and adjacent part of the eye muscles but to an especially thinner type of muscle fibre. Numerous sections were prepared of eye muscles to determine the size of the individual eye muscle fibres and the frequency of such types as could be distinguished.

It was possible to distinguish three groups of muscle fibres according to size. Firstly there is a very thick muscle fibre which tends to occur in bundles of about ten to fifteen. These are not so very numerous. A second type could be classified as of medium thickness. These are by far the most common and compose the greater part of the muscle belly. The thinnest fibres are few in number and are found most frequently towards the margins of the muscle belly. Nevertheless, isolated thin fibres do occur throughout the muscle. The thick fibres are on the average two to three times the thickness of the most slender ones present. There is no sharp transition between the medium and the thin fibres, the extremes of each forming a continuous gradation. Broadly, therefore, two types of muscle fibre are present, a thick and a thin. The presence of fixed contraction waves in each type shows that these differences are a permanent feature of the muscle fibres.

The relationship of the two kinds of nerves to the two kinds of muscle fibre was inferred from observations made on muscle spreads prepared by methylene blue staining, and special examinations were made to determine if these two innervating systems overlapped. Observation alone is not able to exclude such a possibility, but repeated search in this material did not enable us to find any ordinary motor endings on these fine muscle fibres. This opens the possibility that the special fine fibres may be both motor and sensory.

ORIGIN AND COURSE OF THE SPECIAL FIBRES

Boeke had concluded from his experimental investigations that the finer fibres with their endings were mainly derived from the superior cervical ganglion of the cervical sympathetic. The duration of survival of the animals after section of one of the ocular nerves was really too short to be decisive, and the results after removal of the cervical sympathetic were described as indicating a diminution in the number of finer fibres. The author himself appears to have felt that these experiments were inconclusive, for he later designed others for the proof of his theory of the double innervation of striate muscle.

The discrepancy between the interpretation of his morphological observations and mine has already been alluded to. Our own experiments were carried out in the Anatomy Department of the University of Adelaide. In five rabbits the upper portion of the cervical sympathetic trunk including the superior cervical ganglion was removed. The animals were allowed to survive for some thirty days and then killed. The nerves were prepared by intra-vitam staining with methylene blue, and by silver staining. Also the completeness of the sympathectomy was confirmed by dissection. The results obtained convinced us that removal of the superior cervical ganglion on one side had no effect on the number, distribution or endings of these finer fibres. No difference between the two sides was apparent, and it was therefore concluded that these fine fibres did not come from this source, and were not sympathetic fibres belonging to the thoraco-lumbar outflow.

Other possible sources for these fibres were considered. They might belong to the cranial autonomic nervous system. In this case they would presumably belong to the post-ganglionic fibres arising from such ganglia as the ciliary. If this were so they would take origin close to the muscles, and even if other ganglia like the ciliary were present, but unknown because of their microscopic size, the same distribution might be assumed. Thus if the ocular nerves were divided close to the brain those fibres having their cell origin more distal would survive such a section.

Another possibility is apparent since several observers have described the presence of ganglia on the trunks of the ocular nerves. Nicholson in particular in the human foetus counted some thirty cells on the root of the third nerve, and thirteen on its branches in the orbit. He found also some thirty nerve cells on the trunk of the sixth nerve. Sherrington and Tozer cut the sixth nerve in

the monkey, cat and rabbit, and found that about twenty fibres escape degeneration. These cells might be scattered members of the autonomic ganglia stranded in their peripheral migration, or more probably represent in a variable degree the ganglia of the somatic motor ocular nerves present in the embryo but tending to disappear in the adult. Thus they would be like the ganglion of Froreip of the hypoglossal, homologous with the dorsal root ganglia. It is difficult to associate the highly important proprioceptive mechanism of the eye muscles with a system likely to be so variable, and in any case far too inconsiderable for the purpose.

If this fine system of fibres runs in the ocular nerves and retains its characteristic form throughout the whole of its course it is clear that their abundance should make them easily recognisable in the trunks of the ocular nerves. In order to test this possibility numerous preparations were made of these nerves. Some were stained with osmic acid and teased; others similarly stained were sectioned; preparations of the nerves by the silver process were sectioned and all bundles in proximity to the muscles were closely scrutinised for the presence of these fibres. The teased preparations failed entirely to show fine or non-medullated fibres in any number in the trunks of the ocular nerves. Transverse sections of the trunk of the third nerve stained with osmic acid showed numerous medullated fibres with considerable variation in the size of the medullary sheath. A few fine and non-medullated nerves were seen. Assuming these latter belonged to the pre-ganglionic fibres of the ciliary ganglion it must be concluded that this fine system does not exist at the origin of the ocular nerves as a fine or non-medullated system. The examination of nerve bundles cut in proximity to the muscles shows that collaterals frequently arise from medullated nerves. Thus it is concluded that this finer system of nerve fibres if present in the trunks of the ocular nerves runs in these as medullated fibres.

Division of the ocular nerves close to their exit from the brain should be decisive in determining the possibility of these fibres running in the trunks of the ocular nerves. The section close to the brain would leave intact those fibres which belong either to the cells scattered along the trunk or to the more peripheral autonomic ganglia. The operation of dividing the third nerve close to its exit from the brain was attempted on several rabbits. Unfortunately the operation is difficult and the effects severe. In order to elevate the brain sufficiently much bone must be removed. In most cases the survival period was short. Our best case showed a complete division of the third nerve at its exit from the brain at a post-mortem made on the thirteenth day after operation. We hoped for a longer time in which the nerves might degenerate, but the animal was refusing food and it was felt that any more delay might jeopardise the methylene-blue staining. The animal was killed and a vital injection made. The histological picture was excellent. On the non-operated side (the left) a perfect forest of fine fibres with their endings was obtained. On the operated side we had the contrast between those muscles supplied by the third

nerve which had been cut and those innervated by the remaining ocular nerves. Those unaffected by the operation showed fine fibres with their endings, while in the case of those belonging to the third nerve there was complete degeneration of the ordinary motor nerves and also of this finer nervous innervation. It is therefore concluded that this finer system of fibres issues from the brain stem in the ocular nerves and probably in the form of medullated nerves.

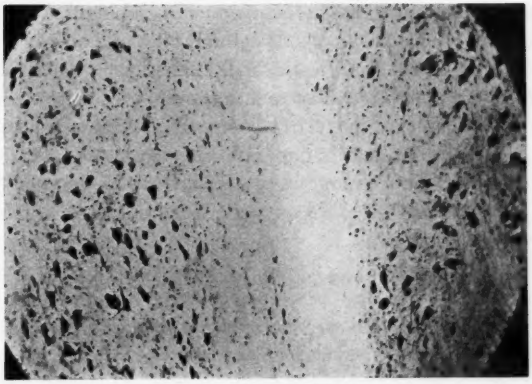

Fig. 2. Transverse section through third nucleus in the rabbit in which the right third cranial nerve was divided.

Right Side. Upper cells are normal. The lower cells show chromatolytic changes.

Left Side. Upper cells show chromatolytic changes. The lower cells are normal.

THEIR SOURCE IN THE BRAIN STEM

From the rabbit which survived for thirteen days after total section of the right third nerve the brain was removed and fixed in alcohol. The portion of the brain stem containing the third nerve nucleus was then cut in serial sections and stained with toluidin blue. The result was an excellent series of sections in which chromatolytic changes were most apparent. These chromatolytic changes affected the third nerve nucleus on the side where the nerve was severed. The third nerve nucleus of the opposite side showed perfectly normal nerve cells. The other nerve accumulations in the neighbourhood such as the red nucleus were perfectly normal.

In the third nerve nucleus the chromatolytic changes affect the whole of the nucleus with the exception of a collection of cells in the most dorsal part of the nucleus. This, however, is degenerated on the opposite side and thus one concludes that the branch to one of the muscles within the distribution of the third nerve of the rabbit undergoes complete decussation.

The nucleus of Edinger-Westphal, which lies at the front of the third nerve nucleus and extends towards the median line, was unaffected by the chromatolytic changes. The nucleus of Darkschewitch, which is lateral to the third

nucleus, also escaped the effects of the section. These results agree with those of other investigators. Winkler has given a full discussion of such investigations. They are of interest as both or either have been invoked as the source of the pre-ganglionic fibres of the ciliary ganglion, and thus the source of the fibres which innervate the ciliary muscle and the sphincter iridis.

From the scheme of localisation in the third nerve nucleus of the rabbit the dorsal collection of cells which shows chromatolysis has been allocated to the levator palpabrae superioris, by the work of van Gehuchten and his collaborators, based on removal of individual eye muscles.

It would be unexpected and against all principles in the architectonics of the central nervous system to expect to find the sensory cells of the eye muscles intermingled with the motor nuclei of this nerve. The arguments advanced and the observations recorded in this paper so far compel us to believe that this finer system of nerve fibres emerge in the ocular trunks as medullated nerves. This further supports the idea already put forward that they are sensory in function though of very different arrangement in detail from the sensory innervation of other muscles. It would be surprising if this special nervous system, possibly sensory in function, arose from cells which were intermingled with the motor cells of the ocular nuclei. Disregarding therefore the chromatolytic changes in the third nerve nucleus itself we can further exclude the Edinger-Westphal nucleus and the nucleus of Darkschewitch.

There remains another possible source, namely the tractus mesencephalicus of the fifth. It is now known that this column contains the proprioceptive fibres which come from the muscles of mastication. Just as the fifth nerve has taken over in the course of evolution most of the cutaneous innervation of the region of the cranial nerves, so perhaps there has been a similar extension in the range of its proprioceptive innervation. The tractus mesencephalicus of the fifth extends well up to the level of the third nerve nucleus. The cells of this column were examined for chromatolytic changes and such changes were found on the right side, that is, the side on which the operation was performed. The tract of the opposite side was quite normal. It is concluded therefore that the cells of origin of this finer system take origin in the upward extension of the mesencephalic tract of the fifth from that portion of it which is on a level with the third nerve nucleus, adjacent to the grey matter about the central aqueduct. The method of retrograde degeneration has its limitations, and further investigations are necessary to prove finally the source of the sensory nerves of the eye muscles, but the present investigation does suggest quite strongly that they start from cells in the mesencephalic tract.

SUMMARY

(1) There are two types of nerve fibre concerned in the innervation of the eye muscles: the ordinary medullated type with motor terminal plates and a second finely medullated or non-medullated, forming several claw-like endings, usually epilemmal, but occasionally hypolemmal.

(2) The medullated fibres are related to thicker muscle fibres, while the non-medullated are related to thinner muscle fibres. It has not been observed that the thinner muscle fibres also receive a medullated ending.

(3) This mode of innervation, if not peculiar to eye muscles, is at any rate restricted to a narrow group of muscles, and does not obtain in the trunk or appendicular muscles.

(4) The fibres composing this finer system leave the brain stem in the trunks of the ocular nerves as medullated fibres. They probably lose their myelin sheaths when nearing their final distribution.

(5) Evidence has been obtained that these fibres have their origin in the cranial extension of the tractus mesencephalicus of the fifth nerve where this is on a level with the third nerve nucleus.

(6) The strong presumption that this special system, in its greater part at any rate, is the sensory supply of the eye muscles is made almost certain if this source from the mesencephalic root of the fifth is confirmed.

I wish to express my indebtedness to Mr J. H. Gray who assisted me in the experimental and observational work entailed in this study.

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THE GROWTH OF THE BRAIN OF THE AUSTRALIAN ABORIGINAL

By H. H. WOOLLARD
Department of Anatomy, St Bartholomew's Hospital Medical College

In a previous paper I described the fissures of the brain of the Australian aboriginal and also determined the ratio of the grey matter to the white.

In the present paper an attempt is made to determine by the measurement of the fissures what areas of the brain are most affected by their development. The results so obtained are compared with similar studies on white brains. Further by comparison with the brain of the new-born aboriginal, using the same methods, a study of the fissures of each area during post-natal growth is made and an estimate of their relative development attempted. Finally some observations on the histology of the principal cortical areas are offered.

The material which forms the basis of the present study consists only of the brain of an aboriginal woman and that of her new-born son. Both died during the process of parturition and it was through the kindness and interest of Dr J. B. Dawson and Prof. Cleland that I obtained the brains. The rarity of such material and the slight prospect of obtaining more must excuse the slender basis of this enquiry. The brains were fixed in 10 per cent. formalin and so suspended that they hardened without deformation.

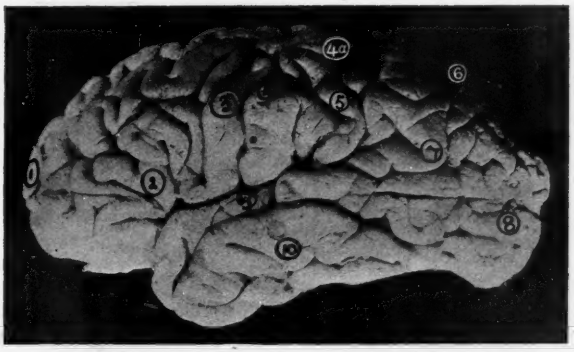
BRAIN OF THE MOTHER

The mother was very stout, about five feet three inches in height, and aged about 43 at the time of her death. Her brain has a total length of 164 mm. and its greatest height is 96 mm., giving a height/length index of 58·5 per cent. It is noticeable that the frontal pole slopes sharply backwards, not having the fullness which is present in the European brain. The temporal pole is elongated and narrow. The superior margin of the parietal lobe is nearly straight, while the occipital lobe appears large and rectangular in form.

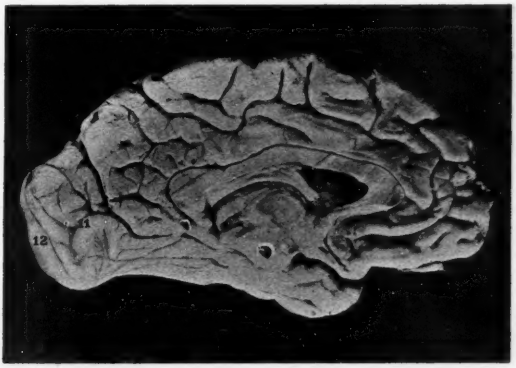
As pointed out in a previous paper, these general appearances are in a large measure the result of the extreme dolichocephaly. An inspection of the stable fissures and gyri calls for brief comment. There is no sulcus lunatus present and the superior temporal convolution appears extremely narrow. This latter feature was noted in the previous study referred to.

BRAIN OF THE INFANT

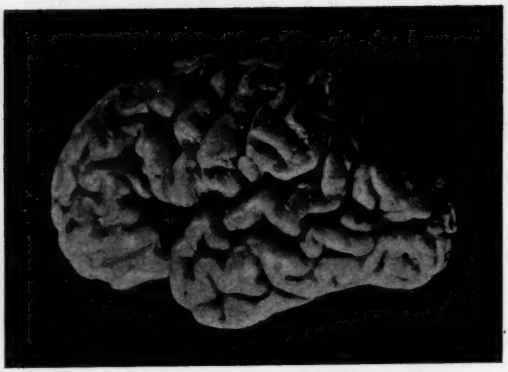
The new-born infant was extremely large, weighing about 12 lb., and the catastrophe at birth was due to this. Though damaged owing to the measures used in delivery, there was no doubt that it was perfectly healthy. It has been established by Spitzka and Karplus that the convolutional patterns have a



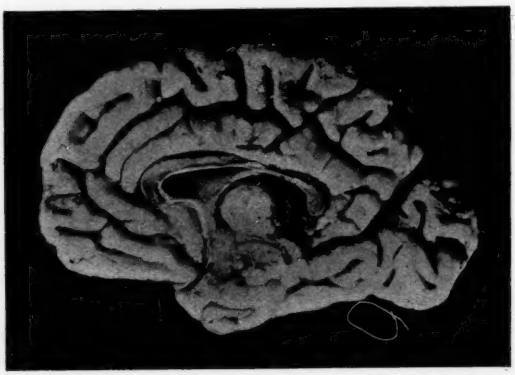
Text-fig. 1. Lateral view of the left cerebral hemisphere of the Australian aboriginal woman. The numbers refer to the actual areas from which the sections of the cortex were taken.



Text-fig. 2. Mesial view of the left cerebral hemisphere of the Australian aboriginal woman. The numbers again refer to the actual areas from which the sections of the cortex were taken.



Text-fig. 3. Lateral view of the left cerebral hemisphere of the full term Australian aboriginal foetus.



Text-fig. 4. Mesial view of the right cerebral hemisphere of the Australian aboriginal foetus.

hereditary tendency to repeat themselves. The present enquiry gains something by being based on the comparison of the mother's brain with that of her son. The maximum length of this foetal brain is 112 mm., while the greatest height is 78 mm., thus giving a height/length index of 70 per cent. Two brains of white foetuses taken at random gave indices respectively of 70 per cent. and 71·5 per cent. The aboriginal foetus, then, exhibits a height/length ratio of the same order as in European brains, and the extreme dolichocephaly is a departure that occurs during the later growth of the brain. Kappers, from a study of brachycephalic brains, concluded that in these the brachycephaly is far less evident in the foetus then in the adult. Perhaps we may therefore surmise that a moderate degree of dolichocephaly is the standard of the human species, and that brachycephaly and extreme dolichocephaly are due to later differential rates of growth.

The degree of exposure of the insula is of the same order as in the white foetal brain. The direction and curvature of the temporal pole is in all respects similar to the white, and the same is true of the parietal area. The occipital pole is drawn out into a slender projection in the aboriginal, but is blunt and rounded in the white foetal brain. In both the white and aboriginal foetus the frontal pole is blunt and rounded.

A comparison of the white and aboriginal foetal fissural pattern discloses no significant differences. Again the superior temporal convolution is definitely smaller than in the white, but the disparity between them is less than in the adult brains.

The superior temporal sulcus resembles the same sulcus in the white foetal brain except that in this instance the fissure is continued into a very well-developed lateral occipital sulcus. This latter is an isolated sulcus in the white brains used for comparison. The central sulcus appeared to be situated more anteriorly in the aboriginal foetus than in the white. A line drawn from the middle of the central sulcus to the frontal pole and to the occipital pole gave in the white and aboriginal foetal brains the following ratios. Taking the distance to the frontal pole as unity the occipital pole distance from the same point in the aboriginal brain is equivalent to 1·2, while in the white brain of the same height/length index the ratio is unity to 0·9. Since broadly it may be stated that the cortical area in front of the central sulcus is concerned predominantly with movement and the area behind and below with sensation these ratios are not without interest.

A detailed comparison of all the principal fissures between the foetuses of both races discloses no differences other than those mentioned. It is to be remarked, however, that there is no sulcus lunatus in this aboriginal foetus.

When the aboriginal foetal brain is compared with the mother's brain, the points noticed may be summarised as follows:

(1) The great proportionate increase in the length of the adult brain as shown by the height/length index, which changes from 70 in the foetus to 58 in the adult.

(2) The occipital pole, which looks like a slender projection in the baby, still retains its protuberant aspect in the mother, though becoming more of a rectangular block.

(3) The frontal pole, which is full and rounded in the foetus, becomes more pointed and less rounded in the mother.

(4) When compared with the white brain it was pointed out that in the aboriginal foetus relatively more of the cerebral hemisphere was contained in the posterior half of the brain behind the central sulcus. If the amount in front be represented by unity 0·9 is caudal to the central sulcus in the white foetus, 1·2 in the aboriginal foetus, and 1·3 in the aboriginal woman. Thus it would appear as if growth were more marked towards the occipital pole than towards the frontal pole.

(5) The superior temporal gyrus tends to be pinched out in both the mother and the child. In the mother the lateral occipital sulcus is almost cut off from the superior temporal sulcus. They were continuous in the child.

In general it may be said that the foetal brain exhibits only slight differences from the white foetal brain, but during growth it departs from the common form mainly by a disproportionate growth in length which gives to the adult brain a very low height/length index. The growth would appear to follow the general law of polar growth, but there is some evidence to be obtained from changes which occur in the interval between birth and maturity that the growth is greater towards the occipital pole and less towards the frontal pole.

General Data on the Aboriginal Brains

Height of woman	5 ft. 3 in.
Total brain weight with membranes	1050 gm.
Weight of cerebellum with membranes separated at the level of the fifth nerve	118·2 „
Brain stem and cerebellum divided at interval between corpora quadrigemina	137·3 „
Weight of right hemisphere, membranes removed, ventricles empty	442 „
Same, with membranes	449·5 „
Weight of left hemisphere, as above	453 „
Same, with membranes	460·7 „
Ratio of weight of cerebellum to cerebrum	11 %
Length of mother's brain	164 mm.*
Greatest height	96 mm.*
Height/length index =	58·5
Foetal brain	
Weight of infant at birth	11·8 lb.
A. *With membranes*	
Total brain weight	444 gm.
Cerebellum	24 „
Right hemisphere	204·6 „
Left hemisphere	206·3 „
B. *Without membranes*	
Right hemisphere	184·8 „
Left hemisphere	187·8 „
Cerebellum	20·7 „
Weight of spinal cord	5·3 „
Ratio of cerebellum to cerebrum	11·4 %
Greatest length of foetal brain	112 mm.
Greatest height	78 mm.
Height/length index =	70 %

* Right hemisphere measured in each case.

THE LENGTH AND DEPTH OF SELECTED SULCI

This aspect of the present investigation was suggested by Donaldson's article on the brains of three scholars.

The growth of the fissures appears to be, if not completely, at any rate relatively, independent of other cerebral features. The fissures appear in an orderly sequence which is always the same in all human brains. Their successive development leads to the production of a stable pattern which can always be identified and compared. True there is a later production of secondary diversified unstable fissures which cannot readily be reduced to any appreciable system.

The measurement by Donaldson of the length and depth of selected fissures in the four principal areas (the frontal, the parietal, temporal and occipital) of the brain disclosed several interesting facts. The area obtained by the product of the two measurements length and depth, which is about equal to one-fifth of the whole cortex, varies independently of the mass of the brain. This fact shows very well the independence of the development and growth of the fissures, since in all other respects the brain exhibits the most constant relation in the proportional weights of its various parts. In addition there is also a constant ratio of the amount of grey matter to white. This was established for a variety of brains by Kappers and the same holds in the aboriginal brain.

Donaldson compared the fissural dimensions of the two hemispheres and discovered that a reduction in one part of the fissural dimensions was compensated by an increase in another part, and therefore concluded that the cortical area so measured bore a constant ratio to the total cortex available for function.

If we can regard the fissures as having a growth characteristic peculiar to themselves and independent of other cerebral characters it becomes of some moment to enquire what meaning can be attached to the fissures. There is no evidence to suggest that any particular kind of mental performance is associated with the length and depth of the sulci in any particular area. Study of the pattern of the fissures has so far been fruitless in suggesting any relation with the level of mental performance. It is perhaps most probable that the fissures represent the segregation of neurons according to functional groups. Indeed of some we know this to be the case, but in others the meaning still escapes us. At the moment then the most that can be asserted is that the fissures represent a relatively independent growth capacity of the cerebral cortex. It has been argued that good fissural growth would represent the existence of favourable nutritional conditions, and to that extent would supply some measure of the physiological factors that must co-operate in mental performance, but it is difficult to see why this should apply to fissural growth more than to any other feature that might be chosen. Since the growth of the fissures must influence the extent of cortex in the several areas of the brain the data derived from their length and depth enable us to institute comparisons between the principal areas of different brains.

The following data have been prepared of the brains of the mother and the foetus:

	Left hemisphere			Right hemisphere		
	Length	Depth	Area of cortex	Length	Depth	Area of cortex
MOTHER						
Frontal area	mm.	mm.	mm.	mm.	mm.	mm.
S. front. mesialis	89	8	713	92	9	828
superior	155	14	2170	126	15	1890
medius	—	—	—	20	4	809
inferior	83	13	1079	48	14	570
S. precentr. superior ...	41	15	615	30	10	300
S. rostralia	48	7	336	31	4	124
S. cinguli	92	7	644	68	4	272
S. pars marg. cing. ...	52	11	572	50	9	450
S. ramus ant. horiz. ...	16	9	144	19	7	133
desc. diag. ...	33	7	231	28	13	364
S. precentr. inf.	44	12	528	64	13	832
Parietal area						
S. centralis	120	13	1560	103	16	1648
S. postcentr. inf.	42	12	504	44	14	616
sup.	39	14	546	48	13	624
S. intrapariet.	51	20	1020	29	16	464
S. pariet. sup.	48	13	624	38	11	418
S. parieto-occip.	57	14	798	51	16	816
S. ramus post. Sylvian fiss.	145	18	2610	126	20	2520
Temporal area						
S. temp. sup.	95	14	1274	81	16	1296
med.	58	8	464	137	7	959
Occipital area						
S. calcarinus	74	12	888	79	10	790
S. occip. trans.	40	13	520	33	13	429
lat.	41	8	328	35	7	245
FOETUS						
Frontal area						
S. front. mesialis	60	6	360	60	6	360
medius	25	10	250	74	8	592
superior	54	11	594	58	9	522
inferior	59	11	549	30	7	210
S. cinguli	84	7	586	64	6	384
S. pars marg.	34	7	238	41	7	287
S. rostralia	34	6	204	26	4	104
S. precentr. superior ...	34	10	340	31	6	248
mes.	12	5	60	—	—	—
inf.	29	11	319	42	10	420
S. ramus ant. horiz. ...	11	10	110	10	5	50
ascend. diag. ...	13	3	39	14	6	84
Parietal area						
S. centralis	63	11	693	66	10	660
S. postcentr. inf.	33	14	462	37	13	481
S. parieto-occip.	35	12	420	38	11	378
sup.	16	10	160	25	6	150
S. intrapariet.	30	17	510	36	14	504
S. Sylvian post.	74	13	962	60	15	900
S. postcentr. sup.	22	9	198	24	9	216
Temporal area						
S. temp. sup.	80	10	800	78	13	1014
med.	49	6	144	50	7	350
Occipital area						
S. calcarinus	54	12	648	52	11	572
S. occip. trans.	25	8	200	29	8	232
lat.	24	11	264	16	11	176

Average Length of Sulci in mm.

	Frontal	Parietal	Temp.	Occip.	Total
Mother	639	471	184	151	1445
Foetus	366	281	166	100	913

Average Depth of Sulci in mm.

Mother	10	15	11	10·5	46·5
Foetus	8	12	9	10	39

Average Extent of Cortex in mm.

Mother	6390	8706·5	2024	1585·5	18706
Foetus	2919	3347	1154	1046	8466

Average Extent of Cortex in percentages

Mother				
Length	44	32·6	13·4	10·4
Extent of cortex	37·4	41·4	11·2	9·2
Foetus				
Extent of cortex	34·4	39·6	13·6	12

Comparison of the Hemispheres. Extent of Cortex and Length of Sulci in mm.

	Frontal		Parietal		Temporal		Occipital	
	Length	Extent of cortex	Length	Extent of cortex	Length	Extent of cortex	Length	Extent of cortex
Woman, Right	586	5835	439	7106	149	2255	147	1464
Left	692	7559	502	7762	218	1738	155	1736
Foetus, Right	452	2901	276	3289	126	1364	97	980
Left	450	3291	286	3405	104	944	103	1112

The total length of the sulci in the adult aboriginal female brain herein measured is 1445 mm. This figure may be compared with the female in Donaldson's series O.W.S. This brain weighed just over 500 gr., while the aboriginal hemisphere was approximately 450. The length of the sulci in O.W.S. is given as 1850, a difference of some 400 mm. This is the more significant when it is remembered that the aboriginal brain is extremely dolichocephalic and therefore favourable to growth in length of sulci. Turning to the depth of the sulci O.W.S. gives an average total depth of 51·95, while the aboriginal woman gives an average depth of 46·5. If we divide the total length of the sulci into the total area of measured cortex an average depth is obtained for O.W.S. of 13·8, and for the aboriginal woman of 11·8. In general the white woman has 20 per cent. advantage in length of sulci, and 14·5 per cent. in depth of sulci.

O.W.S. gives an average extent of cortex of 25,528, while the aboriginal woman gives 18,706. Again the comparison is to the disadvantage of the aboriginal woman and amounts to 33 per cent. In this connection it is to be observed that the extent of the cortex obtained by this method for E.E.S., who is described as an eminent neurologist, is given as 16,409, a quantity actually less than in the aboriginal woman, while that of E.S.M., one of the scholars, only amounts to 19,653.

If we now turn to the distribution of the extent of cortex in the different areas, we find that in the parietal areas the measured cortex in the aboriginal

woman is 41·4 per cent. of the whole measured cortex, while in the white woman O.W.S. it is 35·9 per cent. In the frontal area they are respectively 37·4 per cent. and 38·3 per cent., in the occipital 9·2 per cent. and 6·6 per cent., and in the temporal area 11·2 per cent. and 19·2 per cent. From the figures given by Donaldson it appears that in the aboriginal brain the percentage area of measured cortex was lower in the frontal region than the six brains studied by him; higher in the parietal areas in all cases; approaches the scholars' brains, and exceeds the three Southard brains, in the occipital area; and is particularly unfavourable in the temporal region. The lowest value given in Donaldson's series is 18 per cent., while in the aboriginal woman 11·2 per cent. is the relative proportion of the temporal area.

It seems as if some significant aspect of the aboriginal brain has been here brought to light. It has been recorded in the previous study that the temporal area appeared as if the convolutions had been pinched out, and the same thing has been noticed here in the mother's and infant's brain. It now appears that not only are the convolutions reduced but also that the growth in length and depth of the sulci is deficient. The disparity is seen to some extent in depth, but particularly in length. If the length, depth, and extent of the measured cortex of the temporal area in foetus and mother be compared it will be seen that two areas, the occipital and the temporal, relatively diminish as the brain grows. The occipital still retains the same proportions as in the white brains, while the temporal falls far behind.

Thus by observation and measurement the conclusion emerges that the relative failure of the growth of the temporal area is an important feature of the aboriginal brain.

The comparison in growth of the length and depth of selected sulci between mother and foetus shows that the length has increased most in the frontal and parietal regions, least in the occipital and temporal regions. The occipital increase, however, exceeds that of the temporal. The amount of increase is practically the same in the frontal and parietal regions, while in the temporal region it is only half as great as in these two. The occipital growth is intermediate between these two. Expressed as the natural logarithms the amounts of increase in length are: frontal 5·61 (75 per cent.), parietal 5·24 (67·6 per cent.), occipital 3·93 (51 per cent.) and temporal 2·89 (10 per cent.). In regard to the depth the increase is more regularly distributed, except in the occipital area where the increase is slight.

In regard to the extent of cortex measured by the length and depth of selected sulci in the four principal areas, the amount of growth in extent follows very much the increase in length except that the temporal shows a greater increase than the occipital. The relative amounts can perhaps be best expressed by tabulating the square roots of the differences of the extent between mother and foetus in the four principal areas. This gives the frontal 58, the parietal 58, the temporal 29·5, and the occipital 23·2. Thus the frontal and parietal areas exhibit the same amount of increase. It would appear from

Donaldson's results and those of other observers that much greater growth occurs in the frontal than in the parietal area in the European brain. In general the law of brain growth has been formulated as a polar growth continuing longest at the frontal and occipital poles. The above analysis then shows a difference in the aboriginal brain, for the parietal area has grown almost to the same extent as the frontal region. The amount of growth in the occipital region is little, yet we have seen that its percentage area of the total measured cortex places it among the best of the European brains. This percentage of the total area of measured cortex is still greater in the foetal brain. We conclude then that the growth of the occipital area is peculiarly precocious in the aboriginal brain. In addition to the poor growth of the occipital region from birth onwards the relatively slight growth of the temporal region reduces the percentages of this measured area. Thus it seems that the occipital region is precocious in growth, while the temporal is poorly developed at all ages.

THE SIGNIFICANCE OF THE TEMPORAL REGION

It is but natural to enquire if any special significance attaches to this failure of the temporal region, a failure which appears to be established both by development of its sulci and by observation of the convolutions.

An enquiry into the mental achievement of the aboriginal might betray wherein his deficiency resided. However, great difficulties are encountered in making any analysis. It is customary to refer to him as the most primitive member of the human species. The craniometrical studies of Morant do not support this notion altogether, and Morant concludes from his studies that he is only one among several primitive races and has no special affinity with any fossil human type. Cultural studies place him about the Aurignacian level (E. O. James), with a complex social organisation, but with little control over his environment, and no evidence of any provision for future needs, a fact the more remarkable considering the wide fluctuations in food supply from season to season in his country.

The estimates of different observers vary from considering him merely a beast, to supposing him capable of almost any achievement given the opportunity. I have tried with Dr Pulleine of Adelaide to arrive at some more definite result. There are few opportunities of testing any considerable number of pure-blooded aboriginal children by the Binet-Simon intelligence tests, but some are available in Mission schools. We have made some tests and intend to enlarge this enquiry later. In addition we have collated evidence from schoolmasters, farm-managers, and others. We have tried to assess the results of games wherein success depended on the perception of some simple relation, their ability to solve easy arithmetical problems relating to their interests, and to draw conclusions from various interrogations of young adults, etc. Provisionally we suggest that the aboriginal intelligence is about that of an 8-year old child. There is of course great individual variation. Actual testing suggests that the range of visual acuity does exceed that of the white man.

We believe, therefore, we have sufficient evidence to justify the statement that the level of mental performance of the aboriginal is about that of our own least efficient performers. We have no evidence which enables us to dissect the particular element, if such there be, that conduces to this level. Perhaps the results obtained by students on anthropoid behaviour have some relevance to this problem. Köhler, Yerkes, and others have presented evidence from the study of the chimpanzee of his ability to solve problems depending on visual stimuli. There seems to be no reason to suppose that we have any advantage which depends on peripheral visual discrimination. From the results they obtained it is suggested that thought processes, albeit rudimentary, but essentially similar to our own, occur in the brain of the anthropoid. The point which bears on the present problem is the utter inability of the anthropoid to use or acquire any sort of language. All efforts to teach him one or two simple words appear to have ended in complete failure. It is difficult to imagine what kind of thought processes can go on in the absence of any kind of language. The power of symbolic formulation that depends on this auditory cortex, i.e. language, is then the next great achievement in human evolution. This present study suggests that the neural basis of this mode of symbolic formulation is of a more restricted character than in the white brain and is the factor that determines the cultural level of the Australian aboriginal. He is therefore deficient, not in the sense attaching to feeble-mindedness, but in the sense that his powers of symbolic formulation are definitely limited by the deficiency in growth of the auditory area of his brain.

It is to be remarked that Bean has presented evidence of a deficiency of growth in the temporal region of the brain of the American negro and Hrdlička has found a similar lack in the growth of the same region of the skull.

Attention has been drawn by Elliot Smith to the expansion of the temporal area of the brain of fossil man disclosed by the study of intra-cranial casts. We see then emerging in fossil man the neural basis of the new mode of symbolic formulation, and because of its newness subject to more than the ordinary amount of variation. It is therefore reasonable to expect that the amount of temporal cortex might be the physical basis of our ordinary distinction of primitive and advanced races.

The present study adds thus a few points to the general story of mental achievement. The early development and the absolute and relative amount of occipital cortex afford evidence of the great importance of vision in the evolution of man and suggest why in primitive man symbolic formulation is mainly derived from visual perceptions. The expansion of the auditory area adds a new mode of symbolic formulation reaching different levels in different races. These events have of course their repercussions throughout the rest of the cerebral cortex and so there is a concomitant increase in parietal and frontal cortex. With the full development of the symbolic formulation dependent on the temporal cortex there occurs the last event, the expansion of the frontal

cortex, which at a guess might be correlated with the manipulation of material objects in the highest sense.

There is one other aspect of the growth of fissures which is of interest. Donaldson took his heaviest brain as a standard, giving to its measurements the value of 100. By extracting the cube root of the weight and squaring this he obtained a value which might be regarded as the expected extent of cortex. This value was then compared with the observed values obtained by the above system of measurement.

The values for the aboriginal brain treated in this way suggest that the weight of the hemisphere should yield an extent of cortex of the value of 81. The observed value is, however, 60 only. The length and depth of sulci compared with what might be expected are also low.

It is to be remarked that the brains studied by Donaldson do not give values by this method which would rank the brain according to performance. One of the scholars' brains gives an observed value of 57 against an expected value of 99. The results obtained by measuring the length and depth of sulci are by no means highly correlated with mental performance. However, the deficiency of the observed value in the aboriginal brain is to be attributed most to deficiency in length. This is the more remarkable in that it occurs in brains markedly dolichocephalic.

THE HISTOLOGY OF THE CORTEX

Donaldson, from the work done by Sugita and others, has concluded that the number of cells in the cerebral cortex is, within the limits of biological fluctuation, the same for all members of the same species.

The Australian brain is smaller than the white brain and the dimensions of its fissures are such that these produce no greater increase of cerebral cortex proportionately than they do in other brains. If then the cortex of the aboriginal should possess the same number of cells as the white then its cortex should either be thicker or should contain a larger proportion of undifferentiated neuroblasts.

The histological sections of the cerebral cortex which follow have been examined for evidence on these points. It may be stated here that the cortex of the aboriginal brain is thinner than that of the white. Cell counts have been made over a large number of sections from different parts of the cortex and the enumerations have been compared with similar sections from white brains and also with counts made from published photographs such as those of Economo. In all cases care was taken, of course, to compare areas from the same level of the cortex and brought to the same magnification. The results so obtained were such as to convince me that the closeness of the packing, the degree of differentiation, and the size of the cells, were much the same in the two kinds of brain and that there must be, therefore, fewer cells in the cortex of the aboriginal. This result is of course in conformity with the ratio of the grey matter to the white.

OBSERVATIONS ON THE INDIVIDUAL AREAS

The position from which the cortex was taken for the making of the sections is shown by reference to text-fig. 1.

Area 1, the pre-frontal area, is difficult to measure, for most sections are placed somewhat tangential to the cortex. As a matter of fact the width arrived at by measurement of what appeared the most suitable area came to 2 mm. This happens to be identical with the value arrived at by Bolton for the same area. The individual laminae show the following measurements:

	mm.
Lam. zon.	= 0·42
Lam. supragran.	= 0·83
Lam. gran. int.	= 0·24
Lam. infragran.	= 0·54

Thus the measurements accord very well with those obtained by Bolton in a normal woman whose brain weighed 539 gr. for the right hemisphere and 515 gr. for the left hemisphere. They are greater than in another case of his (a female, aged 22, brain weight, right 469 gr., and left 465 gr.). In this case the brain weights are almost identical. Bolton has also published a series of microphotographs of the pre-frontal cortex at various ages. Inspection of these alongside the accompanying microphotograph, as well as actual counts of cells over areas of the same size in normal white brains, suggest the conclusion that there are more cells per unit area in the aboriginal cortex than in the white. This difference in number appears to be due to the greater frequency of small cells in the aboriginal cortex than in the European brain.

Area 2. Intermediate pre-central area. This portion of the cortex studied in the region of the pars triangularis conforms to the description of this area. There are no data available at the moment with which we can compare this area either in the extent of the cortex or the width of the individual laminae. It corresponds to Brodmann's regio frontalis inferior and lies outside the pre-central area in his account. Campbell includes it in the intermediate pre-central area.

The actual microphotograph (Plate I, fig. 6) failed to include the whole of the lamina zonalis. The external granular layer is very broad and the lamina pyramidalis is distinguished by the presence of large pyramidal cells. In the infra-granular layer medium-sized pyramids are present. The total width of the cortex is 2·5 mm., which agrees with the width given for this area by Economo. On the whole the granular layers are moderately well developed and better so than in Campbell's picture of the intermediate pre-central area. It resembles Campbell's frontal area. There are no giant pyramids present.

The actual dimensions of the individual layers are as follows:

	mm.
Lam. zonalis	0·16
Lam. gran. ext. and lam. pyram.	1·09
Lam. gran. int.	0·32
Lam. infragran.	1·00

If the accompanying microphotograph be compared with fig. 25 (*FDΓ*, area triangularis) of Economo it will be seen that the stratification of the layers is not nearly so sharp and also that there are fewer cells present in the aboriginal cortex. This is especially marked in the case of the lamina pyramidalis. The speech centres in the two races present considerable histological differences.

Area 3. Area precentralis—the motor area. The microphotograph of this area (Plate I, fig. 7) may be compared with fig. 12 of Economo. The magnification of the picture here presented is slightly greater but the enlargements are sufficiently close to make the comparison easy.

The cortex is 3·27 mm. in depth. As is well known, this is the thickest part of the human cerebral cortex and an average of about 4 mm. is to be expected. Economo gives a range from 3·5 to 4·5 mm. Thus it is to be concluded that the aboriginal cortex is thinner in the motor region than is the white brain.

The cellular type shows in the aboriginal a general trend toward the pyramidal form but this transformation is less complete than in the white brain. The external granular layer, for instance, is more conspicuous and broader than in the white brain. The pyramidal change is marked in the third layer of the cortex and in fact, in the sections examined and in the one presented, exceeds that of the lamina ganglionaris, the Betz cell layer. The internal granular layer, though reduced, is a more marked remnant than in the white brain. The portion labelled lamina ganglionaris is pyramidal in form but the Betz cells are much less conspicuous than would be expected. It is hoped to reinvestigate this area in a further examination of the aboriginal cortex.

Cell counts show that the number of cells per unit area is less in this region than in the white brain. Some interest attaches in this region to the ratio of the supra-granular to the infra-granular layers. Bolton has estimated these thicknesses as being in the ratio of 4 to 3 to each other. In the aboriginal cortex the ratio is as 1 to 1.

Thus the present examination of this region of the brain suggests a less marked differentiation of the cortex, a thinner cortex and reduction in the number of cells per unit area.

Area 4. Area postcentralis.

The width of the individual laminae

	mm.
Lam. zonalis	0·28
Lam. granularis ext....	0·28
Lam. pyramidalis	0·61
Lam. granularis interna	0·36
Lam. ganglionaris with lam. multif.	0·50

The total width is 2·2 mm., whereas 3 mm. is the average in the white brain. The reduction in the total width of the post-central cortex is due mainly to reduction in the supra-granular and infra-granular layers. The width of the internal granular layer is practically the same as that given by Economo for the white brain. In comparing sections from the same area in the two races

there is again a lack of precision comparatively in the stratification of the aboriginal cortex. It is interesting that the reduction in thickness of a receptive area like the post-central cortex should occur not in the primary receptive layer but rather in those parts of the cortex which link the receptive area to adjacent and more distant parts of the nervous system.

Area 5. From the inferior parietal area—the gyrus supra-marginalis.

Area 6. Superior parietal area. Taken from the superior parietal region. This resembles very much the supra-marginal and angular areas. The supra-granular layers are well marked while the infra-granular laminae are not so well developed as in the angular area, for instance. The cortex is here 2·03 mm. in thickness, while it is nearer to 3 mm. in the white brain. Again the stratification is not so sharp.

Area 7. Also from the inferior parietal area—the gyrus angularis.

The piece of cortex taken from the area labelled 5 in text-fig. 1 measures 2·25 mm., while the piece from the area labelled 7 in the same figure is 2·56 mm. in width. They resemble each other in having a well-marked lamina pyramidalis and internal granular layer. The angular area is the thicker and this is due to the greater thickness of the supra-granular layer. In the white brain these areas are nearly 3 mm. in thickness and are therefore thinner in the aboriginal brain. They also differ in being not so well stratified though agreeing in their general conformation.

Area occipitalis. Reference to the numbers 8, 11 and 12 on text-figs. 1 and 2 will show that these have been obtained from the following areas:

8, Lateral occipital area—Microphotograph, Plate II, fig. 12,
11, Posterior calcarine area—Microphotograph, Plate III, fig. 13,
12, Anterior calcarine area—Microphotograph, Plate III, fig. 14.

In this particular aboriginal brain there was no sulcus lunatus. Nevertheless the visual cortex is present on the lateral surface. Reference to the microphotograph (Plate II, fig. 12) actually shows the two divisions of the internal granular laminae undergoing fusion.

In the sections from area 12 the structure shows a universal small-celled cortex in which can be distinguished the inner and outer granules belonging to the stria of Gennari.

In the sections from area numbered 11 in the posterior calcarine area the structure is not so obviously that associated with the visual area. It is 1·56 mm. thick.

In the sections taken from area 8, the lateral occipital area, the structure is that typical of visual cortex. Comparison with the sections taken from a European brain shows that the thickness is much about the same. In each case the anterior calcarine area measures about 2 mm. Though both consist of the same type of small granular cells there are more per unit area in the aboriginal area than in the white brain, showing that the packing is much closer in the former.

Thus the visual area of the aboriginal brain is not only more extensive

actually than in the white brain but has the same thickness; the same, even if not more so, characteristic histology; and possibly even more cells per unit area. When it is remembered that everywhere else the aboriginal cortex is thinner and poorer in cells than the white it becomes obvious how important visual perception must be in the mental life of the primitive Australian.

Area temporalis. The microphotograph, Plate III, fig. 15, corresponds to area labelled 9 on text-fig. 1, and is taken from the superior temporal convolution. The microphotograph, Plate III, fig. 16, corresponds in the same figure to area 10 and is taken from the middle temporal convolution.

Our own examinations of the same areas in the white brain gives us a depth for the cortex of the superior temporal convolution of 2·9 mm. while Economo gives figures of 3 mm. and over. Therefore we conclude this area is much more undeveloped in the aboriginal brain. Furthermore both inspection and counting confirm the impression that the number of cells per unit area of the cortex is less in the aboriginal brain than in the white.

Further measurements showed that the ratio of the infra-granular layers to the supra-granular in the aboriginal was as 7 to 4, while in the white the thicknesses of these two layers were as 5 to 6. That is to say in the aboriginal brain the outer laminae are thinner than in the infra-granular, whereas the reverse is the case in the white brain.

Finally, cell counts per unit area confirm the impression obtained from inspecting sections of these areas from the brains of the two races that there are fewer cells per unit area in the aboriginal brain.

The sections from the middle temporal area more nearly resemble the same area in the white brain.

Thus, in contrast with the occipital area, the temporal area has not undergone any considerable differentiation and this is in harmony with conclusions arrived at in the earlier part of this paper.

SUMMARY

(1) The brain of the Australian aboriginal foetus in its general conformation resembles the foetal brain of the white.

(2) The extreme dolichocephaly of the adult is due to later unequal rates of growth.

(3) The dimensions of the cortical fissures in the principal areas of the adult brain indicate that absolutely and relatively the occipital area is the most developed; that the parietal and frontal areas are moderately developed, the frontal, however, falling behind that of the white; while the temporal area lags very far behind that of the white.

(4) Comparison of the dimensions of the fissures in the aboriginal foetus and adult indicate the precocious development of the occipital area and its relatively great extent. The backwardness of the temporal area is also evident.

(5) It may be said then that the occipital area is the most important neural basis for symbolic formulation in the aboriginal cortex.

(6) The order of development in the principal cortical areas in man is first the visual area, later the temporal area; with each of these is correlated expansion in the parietal and frontal areas; the frontal area is the last of all to show its characteristic human development.

(7) The histological examination of the cortex shows that the degree of cell stratification is less well established than in the white brain except in the visual area.

(8) Everywhere the cerebral cortex is thinner than in that of the white except in the visual area.

(9) Though a sulcus lunatus may be absent the striate area extends onto the lateral occipital cortex.

(10) The number of cells in the aboriginal cortex is both absolutely and relatively fewer than in the white cortex.

(11) The facts elicited in the presented study afford at least an approximate neural basis for the cultural level of the Australian aboriginal as well as an explanation of his special aptitudes such as those based on visual symbolisation.

For much help in the work involved in this study I wish to express my indebtedness to Miss M. Flecker, of the Medical Faculty, University of Adelaide.

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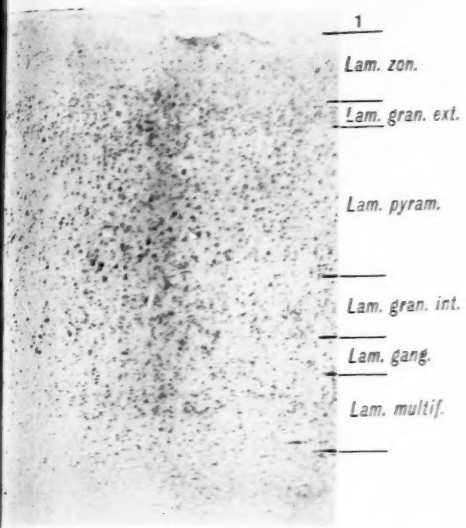

Fig. 5

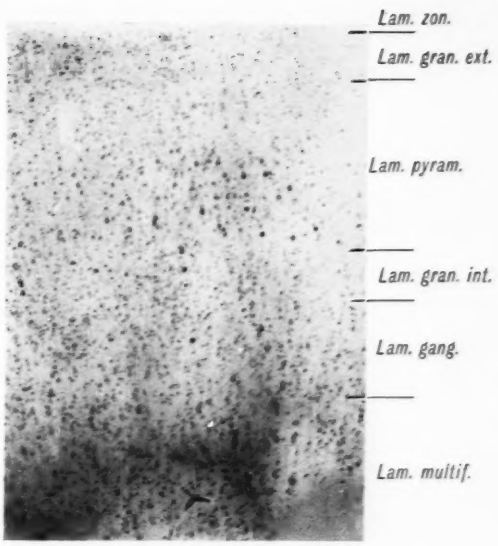

Fig. 6

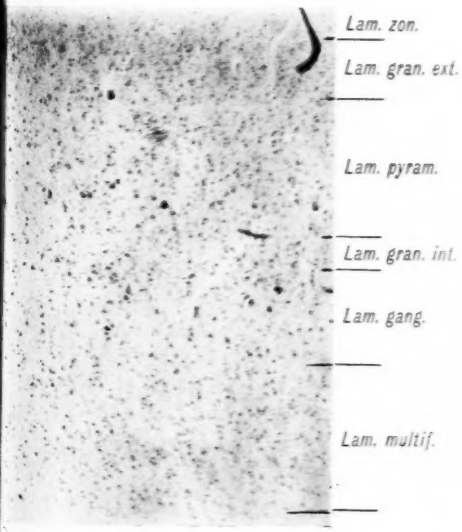

Fig. 7

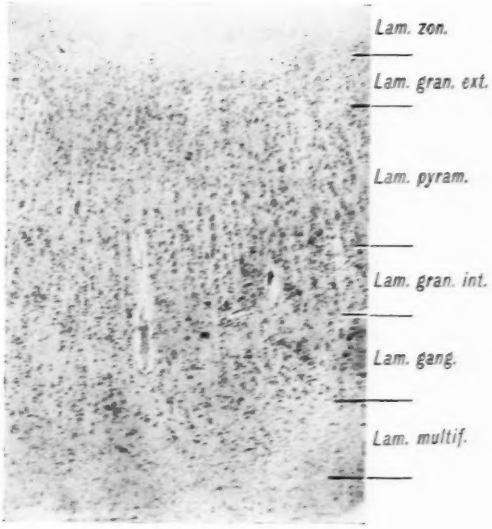

Fig. 8

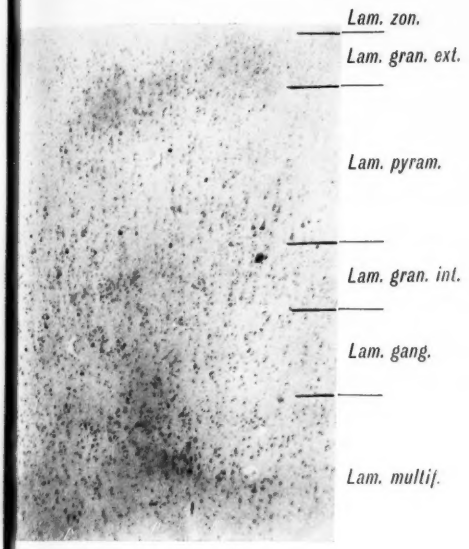

Fig. 9

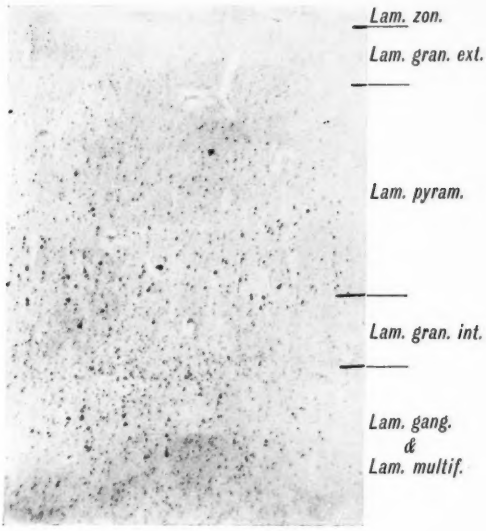

Fig. 10

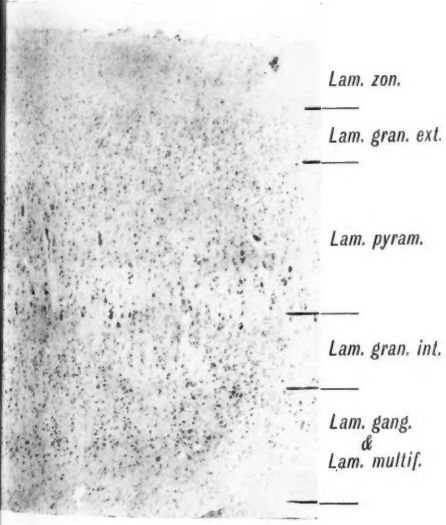

Fig. 11

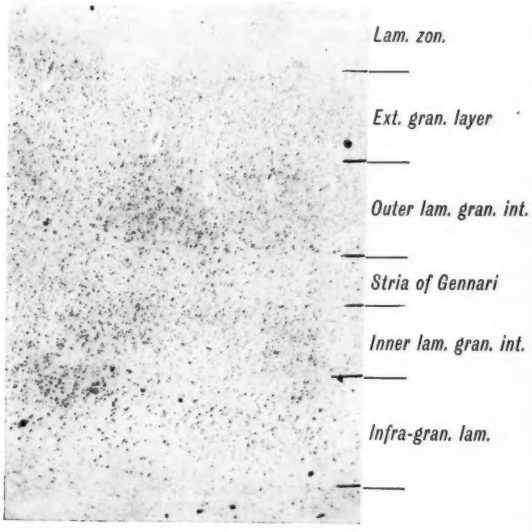

Fig. 12

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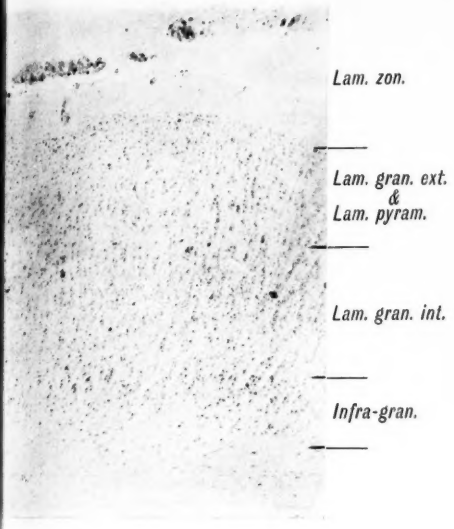

Fig. 13

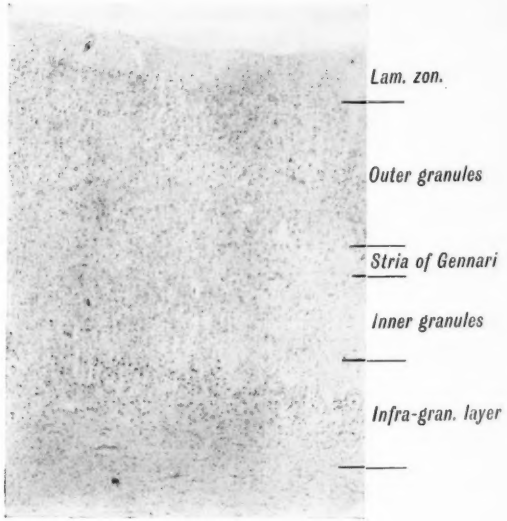

Fig. 14

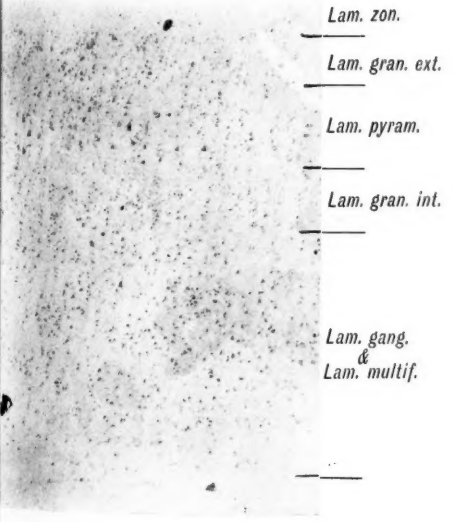

Fig. 15

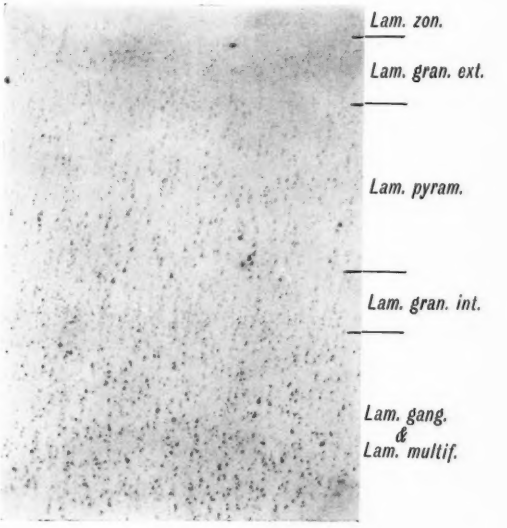

Fig. 16

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EXPLANATION OF PLATES I TO III

Fig. 5. Area pre-frontalis. × 67. Australian aboriginal brain.
Fig. 6. Intermediate pre-central area. Pars triangularis. × 67. Australian aboriginal cortex.
Fig. 7. Pre-central cortex. Motor area. × 47·5. Australian aboriginal cortex.
Fig. 8. Post-central area. × 64. Australian aboriginal.
Fig. 9. Area supramarginalis. × 64. Australian aboriginal brain.
Fig. 10. Area angularis. × 64. Australian aboriginal cortex.
Fig. 11. Superior parietal area. × 64. Cortex. Australian aboriginal brain.
Fig. 12. Lateral occipital area. × 64. Australian aboriginal cortex. On the left the two divisions of the int. gran. layer are fusing together.
Fig. 13. Post calcarine area. × 64. Australian aboriginal cortex.
Fig. 14. Anterior calcarine area. × 64. Australian aboriginal cortex.
Fig. 15. Superior temporal convolution. × 64. Australian aboriginal cortex.
Fig. 16. Middle temporal convolution. × 64. Australian aboriginal cortex.

THE DEVELOPMENT OF HEAD-PROCESS AND PROCHORDAL PLATE IN MAN[1]

By J. P. HILL and J. FLORIAN

From the Department of Anatomy and Embryology, University College, London

(PRELIMINARY NOTE)

THIS preliminary note is the outcome of our study of a young human embryo (Dobbin embryo, 960 μ long), which was presented to one of us (Hill) by Dr Roy Dobbin of Cairo. The embryo belongs to the stage characterised by the presence of a head-process with a well-developed chorda-canal. In the reconstruction of the dorsal view of the embryonal shield (fig. 1), the axial formation which extends cranially in front of Hensen's knot is distinguishable into three portions, a caudal portion forming about the caudal half of the entire formation, a very short but broad cranial portion, and between these two, an intermediate portion which narrows back from the latter to pass into continuity with the caudal portion. The caudal portion is formed by a typical chorda-canal, with seven ventral openings into the yolk-sac cavity and a dorsal opening into the amniotic cavity; the cranial portion represents, in our opinion, the region of undoubted prochordal plate, but we find the intermediate region less easy of interpretation. In front of the most cranial ventral opening of the chorda-canal, the head-process continues directly forwards into the intermediate region as a well-marked cylindrical cord. Solid in two sections, it then develops a lumen which extends through six sections before it ends blindly. In front of the just-mentioned canal, two additional lumina, also closed but of much shorter extent than the first, make their appearance in the median cell-cord. It differs from the more caudal portion of the head-process in two important respects: (1) it is accompanied on both sides by thickened bands of mesoderm which are in continuity peripherally with the forward extensions of the primitive streak mesoderm and which we shall

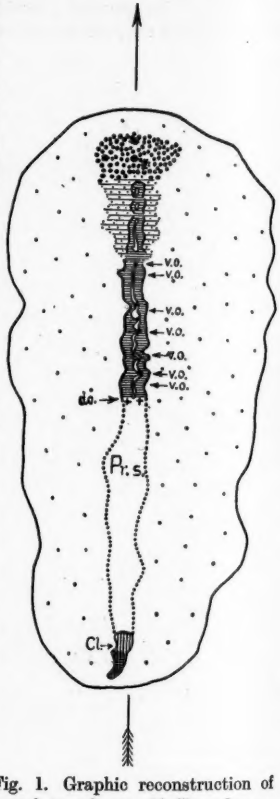

Fig. 1. Graphic reconstruction of embryonal area. *Cl.* Cloacal membrane; *Pr.s.* primitive streak; *d.o.* dorsal opening, *v.o.* ventral opening of chorda-canal.

[1] Communicated to the International Congress of Anatomy, Amsterdam, 1930.

distinguish as the "lateral mesodermal bands"; (2) below it, the endoderm is for the most part distinct, and there is clear evidence that in quite a number of sections it is separated from the median cell cord by mesoderm cells. Cranially the median cell cord and the lateral mesodermal bands pass over into a single, very thick and broad mass, composed of mesodermal cells with which the underlying endoderm is indistinguishably fused. We regard this mass as representing mesoderm derived from the prochordal plate thickening of the endoderm. There are present in it numerous chromatophilic granules similar to those originally described by Bonnet in the prochordal plate ("Ergänzungsplatte") of the Dog.

The precise developmental relations between this undoubted prochordal plate region and what we have distinguished as the intermediate region of the axial formation obviously cannot be determined from the study of one specimen, and can only be finally settled by the study of a close series of well preserved embryos. We have made, however, a very careful study of the intermediate region in our specimen and have examined the corresponding region in various other mammalian embryos, of which an early presomite embryo of Loris (Loris 49 of the collection made by Prof. A. Subba Rau) has proved specially instructive, and the interpretation we have reached is that it represents the cranial segment of the head-process which has undergone differentiation into a median cell cord, the chorda-process, which is in course of becoming luminated and two lateral mesodermal bands, representing so-called "gastral or archenteric" mesoderm. We have no evidence that the prochordal plate participates in the formation of the head-process, and consequently regard that plate as a purely prochordal structure. It is possible, however, that the head-process secondarily grows into the region of the prochordal plate, and that there is an overlap (perhaps only temporary) between the two where they pass into continuity. But even if this is the case, the prochordal plate need not necessarily be regarded as participating in the formation of the chorda-canal, although it might underlie its most cranial segment. We leave this question of overlap quite open, and only call attention to Rossenbeck's remark that the endoderm underneath the most cranial part of the chorda-canal in embryo Peh.$_1$-Hochstetter resembles the endoderm of the "Ergänzungsplatte." The view of Ingalls, that the region we have distinguished as "intermediate," as well as the region we have regarded as the prochordal plate, together constitute the "completion plate" ("Ergänzungsplatte"), we cannot accept. Nor can we accept the view of Rabl that the prochordal plate is simply the most cranial part of the head-process which has pushed forwards into the lecitophor. In our opinion, this view is devoid of any basis of fact, Hill and Tribe(1) having demonstrated the existence in the dog of a mesoderm-producing area in the endoderm (i.e. a prochordal plate) long before the appearance of the other axial structures.

Amongst the described human embryos there are two in which the conditions of the head-process and prochordal plate resemble those in our speci-

men: the Peh.$_1$-Hochstetter embryo (described by Rossenbeck (3)) and the embryo No. 1 of the Department of Anatomy of Western Reserve University, described by Ingalls (2). According to the measurements of the authors, the former ought to be 1·4 mm. long, the latter 1·8 mm.; but it is evident that the difference in their length is due partly to the adoption by the authors of different points of measurement. We have measured the distance between the cranial margin of the prochordal plate and the cranial margin of the cloacal membrane and find that this distance is in Ingalls' embryo about 1·40 mm., in Rossenbeck's embryo 1·36 mm., so that there is practically no difference in length between these two specimens. The primitive streak in Ingalls' embryo is stated to be 0·65 mm. long, in Rossenbeck's specimen about 0·66 mm. The most important difference between them seems to be that in the Ingalls' embryo there are three ventral openings in the proper chorda-canal, whilst Rossenbeck found only two sections in two different regions of the chorda-canal of his embryo where a ventral opening was apparently forming. This difference seems to be of no significance for the estimation of the developmental stage of the specimens; the Dobbin embryo possesses seven ventral openings in the proper chorda-canal (two of them extending through several sections), nevertheless it is certainly younger than Rossenbeck's embryo, the difference in the length of the two being nearly 0·5 mm. It is, therefore, clear that there is great individual variation in this respect and that the disappearance of the ventral wall of the chorda-canal cannot be used alone in the determination of the stage of development of a particular specimen.

The differences in the axial structures under consideration in the Dobbin embryo and that of Ingalls are relatively slight. In the Dobbin embryo, as we have stated, there are three closed lumina in the intermediate axial region of the head-process. In the Ingalls embryo, instead of three cavities, there is one continuous canal in this same region ("completion plate" according to Ingalls, head-process according to our interpretation) which possesses a ventral opening of its own, close to its transition into the chorda-canal proper. It may be suggested that the three separate lumina in the Dobbin embryo would in the course of further development join together to form a single canal, similar to that in the Ingalls embryo.

Apart from the difference in the number and size of the ventral openings, it would seem that Rossenbeck had to deal with very similar structures in his embryo so far as can be judged from his description and figures. We can recognise in the axial formation a caudal chorda-canal with a continuous lumen, possessing two very indistinct ventral openings. In front of this is a region corresponding to our intermediate region in which there is present a median chorda-canal and two thickened bands of mesoderm more or less symmetrically disposed on either side of the latter and broader than those in our specimen. According to Rossenbeck, the lumen of the chorda-canal of this region is directly continuous with that of the caudal portion of the canal. It is worthy of note that, whilst we interpret the lateral mesodermal bands as

derivatives of the head-process, Rossenbeck regarded them as formed by the mesoderm of the "Ergänzungsplatte." Finally there is present a prochordal plate region, the precise limits of which we are unable to determine from Rossenbeck's description.

In respect of the differentiation of the head-process in the intermediate region, we may regard our Dobbin embryo as illustrating the stage in which the chorda-process is in process of acquiring a lumen, inasmuch as the latter is still discontinuous and represented by three isolated portions. In the Rossenbeck embryo, it possesses a lumen which is continuous behind with that of the caudal portion of the chorda-canal, whilst in the Ingalls embryo, the lumen already opens into the yolk-sac cavity just in front of the junction of the two regions of the canal.

In this short preliminary note we need only mention three younger embryos, two of them (Bi. 24 and No. 1285 of the collection of the Department of Anatomy of the University of Manchester) as yet undescribed, the third described by Stieve(4) (embryo "Hugo"). The embryo Bi. 24 was presented by Dr O. Bittmann of Brno to Florian, and is distinctly more differentiated than the embryo "Hugo." No. 1285 of the Manchester collection was generously handed over to us for description by Prof. J. B. S. Stopford.

The "Hugo" embryo (length 635 μ according to our new reconstruction, the median plane of which makes an angle of 64° with the sectional plane) is the earliest human embryo described in which the head-process is clearly developed. It is very short and very indistinctly delimited laterally from the forward prolongations of the primitive streak mesoderm. So far as can be judged from the figures in Stieve's paper, there is an area in front of the undoubted head-process, where the endoderm is not distinguishable from an axial accumulation of more or less loosely arranged mesoderm cells. With this accumulation, the cranial end of the head-process appears to be continuous, but whether or not this area represents a prochordal plate, we are unable to determine with certainty.

In the very well preserved embryo Bi. 24 (length 620 μ), there is a definite but short head-process, the caudal part of which is accompanied by forward prolongations of the primitive streak mesoderm from which it is clearly distinguishable. The cranial part of the head-process is not accompanied by primitive streak mesoderm and passes over in front into an area of thickened endoderm, which we regard as the prochordal plate. It is of comparatively small extent and is not yet very active in mesoderm production.

In the Manchester embryo (length 870 μ) the head-process is still quite short, but it is thicker than that of Bi. 24, whilst the prochordal plate region appears to be more extensive than in that embryo.

Our observations support the following conclusions: The head-process which arises as a forward growth from Hensen's knot and is accompanied by forward extensions of the primitive streak mesoderm becomes distinguishable during development (embryos "Dobbin," "Rossenbeck," "Ingalls") into two

portions, a caudal part which early assumes the form of a typical chorda-canal and a cranial part which undergoes differentiation in the caudo-cranial direction into a median chorda-process (later transforming into a chorda-canal) and two lateral mesodermal bands ("gastral or archenteric" mesoderm). In all the stages we have studied the head-process passes into continuity at its cranial end with the mesoderm of the prochordal plate. Those stages have not furnished any definite evidence of a participation of the prochordal plate in the formation of the chorda-canal.

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CONCERNING THE HOMOLOGIES OF THE HYPOPHYSIAL PIT AND THE POLAR AND TRABECULAR CARTILAGES OF FISHES

By EDWARD PHELPS ALLIS, Jr
Menton, France

The hypophysial pit has generally been considered to be a simple invagination of the external ectoderm, but in October 1923 I expressed my conviction that it was in no part such an invagination, being, on the contrary, the result of the folding or rolling together of two ectodermal surfaces and their fusion with each other excepting along the median line. The two surfaces here concerned were said to cover, the one the anterior surface of the brain and the other the corresponding surface of the visceral arches, and they were accordingly called, respectively, the cranial (cerebral) and visceral surfaces. Whenever these two surfaces fused with each other in the median line as well as laterally, the hypophysial pit was said to be reduced to a solid strand of ectodermal tissue. Other authors had previously concluded that the prehypophysial, but not the hypophysial, portion of the naso-hypophysial canal of *Petromyzon* was, in part (Dohrn, 1881) or in whole (de Beer, 1923), developed in what is in principle this manner; and in December 1923 G. Haller showed conclusively that the hypophysial pit of the Plagiostomi, commonly called Rathke's pocket, is so developed, although he makes no definite statement to this effect. The latter fishes will therefore here be first considered.

PLAGIOSTOMI

In a 1·8 mm. embryo of *Acanthias* the anterior end of the head is shown by Scammon (1911) projecting upward somewhat above the surface of the egg, and the neural plate, which lies directly upon the dorsal surface of the alimentary canal, does not extend to its anterior end.

In a 2 mm. embryo the head is lifted somewhat more above the dorsal surface of the egg, and the neural plate extends to the anterior end of the alimentary canal. The anterior end of the head is completely filled by the anterior end of the alimentary canal.

In a 2·5 mm. embryo the optic vesicles appear as depressions in the anterior portion of the cephalic plate, lying one on either side of the median line. In a 2·7 mm. embryo these two depressions have fused with each other in the median line, this either causing or being the result of a depression of that part of the neural plate that extends from its anterior end to the hind end of the infundibulum. Associated with this, that part of the neural plate that lies between the infundibulum and the medulla oblongata has been somewhat

lengthened and bent downward, through about 90°, in an evenly curved line the convexity of which is directed dorso-anteriorly. The depression of the infundibulum has pressed downward the dorsal wall of the underlying portion of the alimentary canal to such an extent that this part of the canal has the appearance of being a diverticulum of the more posterior portion, directed anteriorly in the level of its floor. This diverticulum lies immediately anterior to that part of the floor of the alimentary canal that will later form the endodermal lining of the bucco-pharyngeal (oral) plate, and it is accordingly called the preoral gut. The part of the canal that lies immediately posterior to this preoral gut is then called the fore-gut, but this term is misleading, for the preoral gut forms the actual anterior end of the alimentary canal.

The anterior end of the roof of the fore-gut is bent downward in an evenly curved line by the pressure of that part of the neural plate that lies between the infundibulum and the medulla oblongata. This part of the plate later increases in length more rapidly than the underlying portion of the wall of the fore-gut, and even in the 2·7 mm. embryo this has caused the neural plate to bulge dorso-anteriorly away from the wall of the gut, thus forming the beginning of the plica encephali ventralis. This plica is generally considered to be developed as a result of unequal growth of the floor and roof of the brain, but in this 2·7 mm. embryo the neural groove is still widely open without a vestige of a roof.

In the 2·7 mm. embryo the lateral edges of the neural groove have already begun to grow upward to form the lateral walls and roof of the brain, and in older specimens the anterior ends of these lateral upgrowths are prolonged mesially around the anterior end of the cephalic plate and meet and fuse with each other in the median line to form the lamina terminalis. This lamina and the infundibular region of the neural plate then have the appearance of forming the anterior wall of the embryonic brain and will hereafter be so referred to. The lamina, when fully developed, is directed dorso-anteriorly and never comes into contact either with the dorsal surface of the alimentary canal or the outer surface of the egg. The angle between the lamina and the dorsal surface of the egg forms what is commonly called the beginning of the head fold, but it seems better for purposes of description and comparison to consider this part of the fold to be formed of two folds here completely fused with each other, a naso-hypophysial fold which lies immediately beneath the brain and a head fold which always lies beneath the alimentary canal.

In early ancestors of all fishes there were quite certainly visceral arches related to the premandibular section of the alimentary canal, and it is here assumed that there was but one pair of such arches. As the roof of this part of the canal was gradually pressed downward by the descent of the infundibulum, the dorsal ends of the related visceral arches were similarly pressed downward, the dorsal and ventral ends of the arches ultimately lying not far from each other and the arches straddling, U-shaped, the lateral edges of the canal. The bending downward of the anterior end of the roof of the

fore-gut similarly carries downward and forward with it the dorsal ends of the mandibular mesodermal arches, and these arches extend from there ventro-posteriorly along the dorso-lateral edges of that part of the floor of the gut that will later become the endodermal lining of the bucco-pharyngeal plate. This shifting downward and forward of the dorsal ends of the mandibular arches must necessarily carry with it the mandibular visceral pouches, and it would seem as if the walls of these pouches must form the lateral portions of the bucco-pharyngeal plate, that plate lying in the floor of the alimentary canal between the ventral ends of the mandibular and premandibular arches.

In later stages the posterior end of the bucco-pharyngeal plate is carried downward by the increase in depth of the alimentary canal, and the plate then has the appearance of forming the anterior wall of the canal, the preoral gut becoming what appears to be a diverticulum that arises from the dorsal surface of the anterior end of the fore-gut, and it has long been known as Seesel's pocket.

In a 6 mm. embryo of this fish described by de Beer (1926) the enclosure of the brain has been completed. The infundibulum has shifted relatively forward and its hind edge now lies at the anterior end of what remains of the preoral gut. The fused naso-hypophysial and head folds extend posteriorly to the hind end of the infundibulum. There the naso-hypophysial fold ends, but the head fold continues onward ventral to the preoral gut and abuts against and fuses with the ventral surface of the fore-gut to form the bucco-pharyngeal plate. There is nothing to indicate definitely in median sagittal sections the limit between cranial and visceral ectoderm, but there is a mass of cells immediately internal to what is certainly the dorsal end of the visceral ectoderm and it is said to be derived from the breaking down of the preoral gut. The mass is directly continuous with the internal surface of the visceral ectoderm and also with the anterior end of the fore-gut, and the notochord runs into it and is there lost. The plica encephali ventralis has been somewhat deepened and projects dorso-anteriorly into the cranial cavity. The brain has thus the appearance of bending downward and backward around the summit of the plica, but there has been no actual further bending downward of the anterior end of the head. The anterior wall of the brain has, however, begun to swing downward and backward around the hind edge of the infundibulum as a transverse axis.

In a 7 mm. embryo also described by de Beer, the plica encephali ventralis has become still more deepened and the anterior surface of the brain has swung further downward and backward. At the hind end of the infundibulum there is, in median sagittal section, a small sharply pointed depression which marks the limit between cranial and visceral ectoderm and indicates the beginning of that swinging together of these two surfaces that gives origin to Rathke's pocket, as explained immediately below. This indentation in the ectoderm thus forms the tip of Rathke's pocket instead of forming, as de Beer concluded, the beginning of its invagination. The mass of cells that in the 6 mm. embryo lay immediately internal to the dorsal end of the visceral ectoderm has been

completely dispersed, excepting only that part of it that forms the central portion of the cord of tissue that connects the premandibular somites of opposite sides.

In a 4·5 mm. embryo of one of the Batoidei, species not mentioned, G. Haller (1923) shows the anterior end of the head bent downward and backward to about the same extent that it is in the 7 mm. embryo of *Acanthias* above referred to, but there is only slight indication of a plica encephali ventralis. The anterior end of the notochord is bent downward in the same curved line as the ventral surface of the brain, as is also the anterior portion of the roof of the fore-gut. The cranial ectoderm extends to the hind end of the infundibulum and there meets at an angle of about 45° the morphologically dorsal end of the visceral ectoderm, the latter ectoderm extending from there in a posterior and slightly dorsal direction to the dorso-anterior end of the bucco-pharyngeal plate. The space between these two ectodermal surfaces is called by Haller the "Kieferaugenspalte," but as it forms the deeper, hypophysial portion of the naso-hypophysial fold, it will hereafter be so referred to.

The tip of the hypophysial fold is, at this stage, directed almost directly anteriorly toward the tip of the bent-down anterior end of the notochord, the latter tip being directed posteriorly and slightly ventrally. Dorsal to the visceral and actually dorsal wall of the hypophysial fold there is a mass of cells similar to that described by de Beer in the 6 mm. embryo of *Acanthias*, and it is said by Haller to have been proliferated from the anterior end of the fore-gut. What persists of the preoral gut is said to lie in this mass of tissue, as does also the central portion of the communicating cord that extends between the premandibular somites of opposite sides, the latter apparently lying morphologically dorsal to the former, but the descriptions are not definite as to this.

In later stages of development, the cranial wall of the hypophysial fold continues its swinging motion backward and upward against the visceral wall of the fold and fuses completely with it excepting along the median line, Rathke's pocket thus being cut out of the fold. This swinging together of the two ectodermal surfaces can only extend to the dorso-anterior end of the bucco-pharyngeal plate, for the visceral wall of the fold ends there. The corresponding point in the cranial wall of the fold lies about midway between the hind end of the infundibulum and the optic chiasma, and this determines the position of the external opening of the pocket.

In an 8 mm. embryo of *Raia*, Haller shows Rathke's pocket completely cut out of the hypophysial fold, in the manner above explained, and directed anteriorly and slightly dorsally. The median portion of the communicating strand between the premandibular somites of opposite sides lies dorso-anterior to the tip of the pocket, between it and the tip of the notochord, but the tip of the pocket is directed morphologically dorsal to both of these structures and hence lies between cranial and visceral tissues. The roof of the fore-gut bends downward at its anterior end and is continuous with the hind end of the visceral

wall of the pocket in a well-rounded angle, the two walls of which lie nearly at right angles to each other. This angle forms the dorso-anterior edge of the bucco-pharyngeal opening, which has already completely broken through. From there the opening extends postero-ventrally along the anterior edges of the mandibular mesodermal arches, those arches being directed postero-ventrally and lying inclined at an angle of about 30° to the horizontal plane. The bucco-pharyngeal opening has the appearance of leading directly into the anterior end of the fore-gut, and the preoral gut, if present, would lie immediately dorsal to the visceral wall of Rathke's pocket and hence appear to be a diverticulum arising from the anterior end of the dorsal wall of the fore-gut and projecting forward in the same direction as Rathke's pocket.

The maxillary processes have not yet been developed in this embryo. The mandibular mesodermal arch extends from above postero-ventrally and is said to present four regions which are called by Haller, from above downward, the Kieferaugenspaltstueck, Oberkieferstueck, Zwischenstueck and Unterkieferstueck. The Kieferaugenspaltstueck is later said to be the pharyngeal element of the arch and it will be hereafter so referred to. It is said to form no part of the upper jaw. The upper and lower jaw segments are said to be the serial homologues, respectively, of the ceratobranchials and hypobranchials of the more posterior arches, this seeming to indicate that Haller considered the angle of the gape to lie at the dorsal end of the Oberkieferstueck, between it and the maxillary process when the latter develops. This is, however, certainly incorrect, for the upper jaw segment of Haller's descriptions is certainly the epimandibula and the lower jaw segment the cerato + hypomandibula. The pharyngeal segments of the arches of opposite sides are directed anteriorly and slightly dorsally and form the lateral walls of Rathke's pocket, and their presence at this stage of development has apparently prevented the cranial and visceral walls of the hypophysial fold from meeting and fusing with each other along the median line. The distal ends of the pharyngeal segments are connected by a transverse bar of tissue which is called by Haller the hypophysial bolster, but as it forms the dorsal border of the bucco-pharyngeal opening it will hereafter be referred to as the bucco-pharyngeal upper lip. It forms at this stage the actually dorsal wall of the external opening of Rathke's pocket, but after the cranial flexure has been reduced and the pocket reversed in direction, it lies postero-ventral to the opening of the pocket. A large transverse vein lies immediately dorso-posterior to it and is evidently the pituitary, and hence the canalis transversus of Gegenbaur's (1872) descriptions of the adult.

A group of procartilaginous cells has appeared in the pharyngeal segment of each mandibular arch and is called by Haller the posterior portion of the trabecula. It is unquestionably the polar cartilage of current descriptions of the adult, and the manner of its development, in the pharyngeal segment of the mandibular mesodermal arch, seems definite confirmation of my conclusion (Allis, 1923) that this cartilage is the pharyngeal element of the inner cartilaginous bar of the mandibular arch.

In a 20 mm. embryo of *Acanthias* described by Haller, the cranial flexure has been somewhat more reduced than in the 8 mm. embryo above referred to, and in connection with it the infundibulum has shifted somewhat dorso-posteriorly relatively to the underlying visceral tissues. As a result of this, Rathke's pocket has been swung upward and backward around its point of attachment to the bucco-pharyngeal upper lip and it is directed dorso-anteriorly at an angle of about 70° to the horizontal plane, its tip still being directed toward the tip of the bent-down crook-like anterior end of the notochord and separated from it by the median portion of the connecting cord between the premandibular somites. The pharyngeal segment of the mandibular arch has been swung upward and backward to the same extent as Rathke's pocket, and its proximal end is directed toward the ventral surface of the notochord, somewhat posterior to its crook-like anterior end. It lies at a considerable angle to the epal segment of the arch, the sigma-shape thus being already established in the dorsal half of this arch.

A mesodermal fold (Leiste), called by Haller the upper-jaw process, is said to have grown forward (actually ventrally) from the anterior edge of the dorsal end of the epal segment of each mandibular mesodermal arch, and to extend forward beneath the eye to the region between the orbit and the nasal capsule. There it turns mesially and ultimately meets and fuses in the median line with its fellow of the opposite side. A large depression is thus formed on the morphologically ventral but actually posterior surface of this part of the brain, bounded laterally and anteriorly by the upper-jaw processes, morphologically dorsally by cranial ectoderm and posteriorly (actually dorsally) by the anterior edge of the bucco-pharyngeal upper lip which has become considerably thickened. In later stages the fusion of the anterior ends of the upper-jaw processes of opposite sides is prolonged progressively posteriorly (actually dorsally) until the optic chiasma is passed. Beyond this point it is only the morphologically ventral edges of the processes that meet and fuse with each other in the median line and this continues until the hind ends of these ventral edges of the processes meet and fuse, excepting in the median line, with the anterior edge of the bucco-pharyngeal upper lip which has grown forward somewhat to meet them. A primarily external space is thus enclosed and forms the anterior portion of the hypophysial cavity, Rathke's pocket opening directly into its hind end and the cavity opening to the exterior through a short median, so-called hypophysial canal.

Two groups of procartilaginous cells have appeared in each upper-jaw process. In the deeper one of the two the anterior portion of the trabecula is said by Haller to develop, this being the trabecula of current descriptions of the adult. The other group lies ventral to the anterior portion of the trabecula and the cartilage that develops in it is called by Haller the upper-jaw cartilage. It is said to be primarily a wholly independent cartilage but to later fuse with the epimandibula, thus unquestionably being the palatine process of the palatoquadrate of the adult. These two cartilages lie definitely anterior to the

mandibular arch and their topographical relations to the infundibular region of the brain and to the dorso-anterior end of the bucco-pharyngeal opening are those that the premandibular mesodermal tissues would normally have if, after being pressed downward by the descent of the infundibulum, the preoral gut had been withdrawn or dispersed. It therefore seems quite certain that these cartilages are of premandibular origin and it is probable that they represent, respectively, the dorsal and ventral halves of the entire arch, instead of being simply the pharyngeal and epal elements of that arch, as I have heretofore considered them to be.

In later stages of development the walls of the hypophysial canal coalesce and so form a solid strand of tissue which extends from the internal surface of the external ectoderm to the wall of the anterior division of the hypophysis. In still later stages this strand breaks down and is wholly dispersed. Its point of attachment to the ectoderm varies somewhat, and may be shifted quite far forward, this evidently being due to a greater forward growth of the bucco-pharyngeal upper lip (hypophysial bolster). When this takes place the strand extends dorso-posteriorly, passing in its course between the polar and trabecular cartilages, and if this were the earliest stage of development known, the preceding ones having been omitted or confused in ontogeny, the hypophysis would probably have been considered to have been developed in relation to a strand of tissue that grew inward from the deeper layer of the external ectoderm.

In these embryos, before the development of the maxillary processes, the mouth opening is pentangular in shape, its ventro-posterior borders being formed by the ventral halves of the mandibular mesodermal arches, its lateral borders by the dorsal halves of the same arches and its anterior border by the frontal surface of the head. The angle between the postero-ventral and lateral borders of either side of the opening lies at about the middle of the height of the alimentary canal and forms the angle of the gape, the angle between the lateral and anterior borders forming the lateral opening of the hypophysial fold and corresponding in position to the lachrymal groove of the mammalian embryo. When the maxillary processes develop, each process projects ventro-mesially from the anterior edges of the adjoining ends of the epal and pharyngeal segments of the mandibular arch, the morphologically anterior edge of the process fusing with the frontal surface of the head and completely closing the lateral opening of the hypophysial fold. This maxillary process of either side is formed by the premandibular mesodermal arch, but the dorsal and ventral ends of that arch have been brought close together by the compression of the related portion of the alimentary canal, as above explained, and it is the angle between the dorsal and ventral halves of the arch, and not the ventral end of the arch, that projects ventro-mesially toward its fellow of the opposite side. There is no mandibular cleft, unless it be that it forms part of the bucco-pharyngeal opening, as it probably does. The premandibular cleft, if it ever existed, must have lain in the median line between the premandibular arches

of opposite sides, and have led from the anterior end of the preoral gut into the hypophysial fold somewhat ventral to its dorsal end. There is, in the Plagiostomi, no such opening between the fold and the canal, but there is in *Bdellostoma* and *Acipenser*, as will be later described.

CROSSOPTERYGII

The early development of these fishes is not known (Kerr, 1919).

In later, larval stages of *Polypterus* the hypophysial canal is said to extend from the roof of the buccal cavity to the cavity of the pars anterior of the hypophysis, thus corresponding to the hypophysial canal of embryos of the Plagiostomi. This canal is said to be present even in the adult *Polypterus*, but I found it completely closed in a 75 mm. embryo of *Polypterus senegalus* and also in several adult *Polypterus* that I examined in this respect (Allis, 1922).

The dermo-palatine of the adult turns mesially at its anterior end and meets its fellow of the opposite side in the median line, thus forming a transverse bar across the ventral surface of the chondrocranium that resembles topographically that formed by the palatine processes of the palatoquadrates of the Plagiostomi; and it will be later seen that it is probably this that has determined the opening of the hypophysial canal in the roof of the buccal cavity instead of on the dorsal surface of the snout.

CYCLOSTOMATA

Bdellostoma

Several early stages in the development of *Bdellostoma stouti* are described by v. Kuppfer (1900), but as he did not have a full series of embryos suitable for sectioning, the development of the hypophysial region is not completely and definitely given either in the figures or the descriptions. Certain features of its development, as given by him, are however important and must be briefly considered.

In the earliest embryo described the anterior portion of the brain is deeply embedded in the dorsal surface of the egg, but separated from it by a scoop-shaped fold of the external ectoderm which extends posteriorly, as a fold open laterally on either side, from the lobus olfactorius impar to the region of the recessus preopticus, the alimentary canal extending forward to the latter point. This fold of this fish thus corresponds to the fold that in early embryos of *Acanthias* I have considered to be formed by the complete fusion of the anterior portions of the naso-hypophysial and head folds. The head fold does not in this embryo extend posteriorly beyond this point. The naso-hypophysial fold is, however, prolonged posteriorly by a median pocket-like extension which forces its way between the anterior end of the alimentary canal and the overlying portion of the brain, and extends as far as the anterior end of the infundibular depression. This pocket-like extension of the fold is called by

v. Kuppfer the primary mouth. It presses against the dorso-anterior corner of the anterior end of the alimentary canal and forces it downward and backward, the apposed surfaces forming a transverse membrane which extends from the floor to the roof of the alimentary canal and is called by v. Kuppfer the primary Rachenhaut

There is said to be no cranial flexure in this embryo, but the infundibulum nevertheless lies below the level of the more posterior portion of the floor of the brain and its ventral surface is presented ventro-posteriorly. The anterior corner of this surface projects ventrally and has pressed against the underlying portion of the alimentary canal, there forming on its dorsal surface an angular depression which lies slightly posterior to the anterior end of the canal. This part of the alimentary canal of this fish is thus strictly homologous with the preoral gut of the 2·7 mm. embryo of *Acanthias*.

In the oldest embryo described by v. Kuppfer, the prehypophysial portion of the naso-hypophysial fold has been completely separated from the corresponding portion of the head fold by the development of longitudinal laminar processes, one on either side, which project mesially and meet and fuse with each other in the median line, thus converting the primarily open naso-hypophysial fold into a closed canal. The head fold has been prolonged posteriorly and abuts against the anterior portion of the ventral surface of the fore-gut, the two apposed surfaces forming a membrane which is the homologue of the buccopharyngeal plate of the Plagiostomi but is called by v. Kuppfer the secondary Rachenhaut. The hypophysial portion of the naso-hypophysial fold has been prolonged posteriorly from the anterior to the posterior end of the infundibulum, and has to the latter the topographical relations of Rathke's pocket. A perforation in the floor of the naso-hypophysial canal leads directly into the fore-gut and is the pharyngeal opening of the canal of the adult.

Comparing the conditions in this embryo with those in the earlier embryo above described, the conditions in the former would seem to have been directly derived from those in the latter by the simple posterior prolongation of the pocket-like extension of the naso-hypophysial fold from the anterior to the posterior edge of the infundibular depression and the breaking through of the primary Rachenhaut. The conditions in early embryos of *Acipenser*, to be described below, strongly suggest that this is what has actually taken place, but the conditions described by v. Kuppfer in embryonic stages of *Bdellostoma* intermediate between the two above referred to are unfavourable to this view. The descriptions of the latter embryos are, however, not complete and definite and are therefore here left out of consideration, the important feature in the present discussion being that the naso-hypophysial canal is always hollow throughout its entire length and at no time represented in any part by a solid strand of tissue.

In the oldest embryos described the anterior end of the naso-hypophysial canal is shown completely closed in median sagittal section. This section must therefore have passed through the septum that in the adult separates the

nasal apertures of opposite sides, these apertures lying on the ventral surface of the anterior end of the snout.

Petromyzontidae

In a 5-day old embryo of *Petromyzon planeri* the anterior end of the head is somewhat lifted above the surface of the egg and the brain is solid (v. Kuppfer, 1894, fig. 1; Plate I). The anterior end of the chordal portion of the floor of the brain is bent downward and the prechordal portion is bent relatively upward, as in the Plagiostomi. The anterior end of the roof of the fore-gut is bent downward in an evenly curved line and the preoral gut compressed, the anterior end of the latter gut extending forward to the region of the recessus preopticus. There is no indication of a plica encephali ventralis in this embryo, and when it later develops it is narrow and slit-like instead of being, as in the Plagiostomi, broad and widely open.

The anterior portion of the naso-hypophysial and head folds are completely fused with each other, as they are in early embryos of *Bdellostoma* and the Plagiostomi, and the so-formed fold extends posteriorly to the region of the recessus preopticus. There the head fold separates from the naso-hypophysial one and is prolonged posteriorly beneath the preoral gut and ends in a broad and shallow buccal depression, the bottom of which later becomes apposed to the ventral surface of the fore-gut to form the bucco-pharyngeal plate. The naso-hypophysial fold is not prolonged, as a fold, beyond the point where the head fold separates from it; but, exactly in the place of the pocket-like posterior extension of the fold in embryos of *Bdellostoma*, there is a solid conical thickening of the deeper layer of the ectoderm, the point of which projects posteriorly between the anterior end of the preoral gut and the overlying portion of the brain. This thickening is generally considered to represent the beginning of a strand-like and wholly independent ingrowth of the cells of the deeper layer of the ectoderm, but its even and unbroken outlines are characteristic of a fold and not of an independent ingrowth of individual cells. Furthermore, comparison with the conditions in *Bdellostoma* and the Plagiostomi, and more particularly with those in early embryos of *Acipenser*, would seem to establish definitely that this thickening was primarily, in ancestors of this fish, a fold, the walls of which have been pressed together and have so completely fused with each other that all indication of the pre-existing cavity has been obliterated. This thickening is later either prolonged posteriorly beneath the infundibulum, or the infundibulum shifts forward above it, and the hypophysis develops in the deeper portion of the strand. It will, therefore, hereafter be referred to as the hypophysial strand.

In later stages, the bucco-pharyngeal upper lip grows forward to the anterior end of the snout, as shown in v. Kuppfer's figures and as fully described by de Beer (1923). It grows forward between the head fold and the prehypophysial portion of the naso-hypophysial fold, completely separating them. It fuses laterally, on either side, with the overlying cranial ectoderm, a deep pit

thus being cut out of the median portion of the primarily open naso-hypophysial fold. This pit is called by de Beer the hypophysial depression, and is considered by him and also by Woerdemann (1915) and G. Haller (1923) to be the homologue of Rathke's pocket, but the development in this fish, when compared with that in *Bdellostoma* and the Plagiostomi, would seem to definitely establish that Rathke's pocket is contained in some part of the hypophysial portion of the naso-hypophysial fold and hence in some part of the hypophysial strand of *Petromyzon*. The pit of *Petromyzon* may therefore be called the prehypophysial pit.

In older embryos the deeper end of the hypophysial strand becomes enlarged, a central cavity appears in it and the hypophysis develops in relation to its dorsal wall, the ventral wall remaining membranous (de Beer, 1926). During metamorphosis this hypophysial cavity becomes prolonged posteriorly beneath the anterior end of the notochord and prolonged anteriorly in the hypophysial strand until it reaches and opens into the bottom of the prehypophysial pit. The naso-hypophysial canal of the adult is thus formed, and it is evidently the homologue of the similarly named canal of *Bdellostoma*, notwithstanding that it is developed in a somewhat different manner and does not open at any time into the underlying alimentary canal.

The development of the mandibular and premandibular mesodermal arches is not particularly described, but it seems evident that the posterior portion of the so-called trabeculo-palatine bar of this fish is developed in the pharyngeal segment of the mandibular arch and is hence the polar cartilage. The premandibular arch is said by Haller to have been carried bodily forward by the marked development of the upper lip of the fish. The anterior portion of the trabeculo-palatine bar evidently develops in this arch and quite probably corresponds to the trabecula of the Plagiostomi together with the palatine process of the palatoquadrate. The premandibular arches primarily encircled the preoral gut, just as the more posterior arches encircle the related portions of the alimentary canal. It would therefore be wholly natural and normal that the premandibular cartilaginous bars of this fish should meet and fuse with each other beneath the naso-hypophysial canal, as the trabeculo-palatine bars actually do both in this fish and in *Bdellostoma*.

CHONDROSTEI

In a figure of a median sagittal section through the head of a 45-hour old embryo of *Acipenser sturio* given by v. Kuppfer (1893) the naso-hypophysial and head folds are shown widely separated from each other by the bucco-pharyngeal upper lip, that lip extending forward to the anterior end of the snout and its anterior end being greatly enlarged to form what v. Kuppfer calls the Haftscheibe. The head fold is simply a broad and shallow buccal depression which v. Kuppfer calls the mouth (Mund). Because of the already completed growth forward of the bucco-pharyngeal upper lip the naso-hypophysial fold has been reduced to a median canal called by v. Kuppfer a pocket (Schlauch).

The cells of the walls of this canal (pocket) still retain their radial arrangement and have not fused with each other, but they have been pressed so closely together that the cavity of the canal is completely obliterated except at its outer and inner ends. The walls of the canal arise from the deeper layer, only, of the external ectoderm, the external layer of the ectoderm passing unbroken across the mouth of the canal but there being pressed inward to form a small median conical pit. The deeper end of the canal abuts against and has completely fused with the dorsal wall of the alimentary canal, and the membrane that must primarily have separated the two canals has completely broken down. A small sharply pointed diverticulum of the alimentary canal extends outward a short distance between the walls of the naso-hypophysial canal and apparently represents the preoral gut. What v. Kuppfer considers to represent this latter gut lies ventral to the bucco-pharyngeal upper lip (Haftscheibe) and hence cannot be the primitive anterior prolongation of the alimentary canal.

The anterior end of the brain curves downward through about 45°, and that part of it that lies anterior to the notochord has been somewhat prolonged. The anterior end of the brain, as seen in median sagittal section, extends from the lobus olfactorius impar to what is apparently the hind end of the infundibulum, is of the same length as the naso-hypophysial canal and abuts against or closely approaches it throughout its entire length. The anterior end of the brain of this fish thus has the appearance of being deeply embedded in the dorsal surface of the egg, as it is in the earliest embryo of *Bdellostoma* above considered, and if in the latter embryo the bucco-pharyngeal upper lip had already grown forward to the anterior end of the snout and the so-called primary Rachenhaut of v. Kuppfer's description had already broken through, the conditions would strikingly resemble those in the embryo of *Acipenser*.

In later stages of development the deeper end of the naso-hypophysial canal becomes separated from the dorsal wall of the alimentary canal and is somewhat prolonged dorso-posteriorly beneath the infundibulum, there becoming enlarged to form the hypophysis, the remainder of the canal breaking down and being dispersed. In these embryos the so-called Haftscheibe shifts somewhat ventro-posteriorly and lies on the ventral surface of the snout and the barbels are said to develop in relation to it, these barbels being considered to be the homologues of the adhesive organs of *Amia* and *Lepidosteus*. It however seems probable that they are the homologues of the maxillary breathing valves of the latter fishes.

The anterior end of the head of this fish not having been lifted above the dorsal surface of the egg, and not being prolonged anteriorly beyond it, it is probable that the pharyngeal segment of each mandibular mesodermal arch is directed dorsally or dorso-posteriorly. The polar cartilage, which develops in this segment, would therefore fuse with the anterior end of the parachordal plate instead of with its ventral surface, and it is so shown by de Beer (1925) in a figure of the chondrocranium of a 5-day old embryo of this fish. Sewertzoff

(1928) however says that this cartilage fuses with the ventral surface of the parachordal plate.

The bucco-pharyngeal upper lip, in growing forward, must necessarily either push apart or disperse the premandibular tissues in which, in the Plagiostomi, the palatine processes of the palatoquadrates are developed, and in *Acipenser* these tissues have apparently been dispersed, for the palatoquadrates of this fish are without definite palatine processes. The cartilage called by Parker (1882) the metapterygoideus, is probably developed in relation to the mandibular arch (Allis, 1930), and hence lies posterior to the bucco-pharyngeal upper lip. It would therefore not be displaced by the forward growth of that lip, and there would be nothing to interfere with its meeting and fusing in the median line with its fellow of the opposite side, as it actually does.

HOLOSTEI

In an early embryo of *Amia* described by Reighart and Phelps (1908) and also by Reighart and Mast (1908) the neural canal still lies flat on the dorsal surface of the egg, the neuropore (lobus olfactorius impar) at its anterior end. As the brain develops, its so-called anterior surface accordingly becomes embedded in the dorsal surface of the egg throughout its entire extent, as it does in *Acipenser* and the Cyclostomata. The ectoderm is thickened at the neuropore, and this thickening extends antero-ventrally to form what Reighart and Mast call the fundament of the hypophysis, but which is more properly the fundament of the naso-hypophysial canal. Immediately antero-ventral to this fundament there is a slight crescentic elevation which forms the fundament of the adhesive organ. Immediately beyond this the buccal depression (stomodaeum) later develops. The alimentary canal extends forward to the region of the crescentic elevation and there presents three evaginations, one median and a lateral one on either side, their outer ends coming into contact with the ectoderm immediately beneath the crescentic elevation.

In later stages the crescentic elevation above described separates into three parts, a median button and a U-shaped elevation on either side, each of the latter of which represents one half of the adhesive organ. The button and the related evagination of the alimentary canal later break down and become dispersed. Each of the lateral evaginations becomes constricted off from the alimentary canal and separates into several parts, each of which acquires an opening to the exterior by the breaking through of the ectoderm with which it is in contact. The buccal depression (stomodaeum) comes into contact with the ventral surface of the alimentary canal posterior to these evaginations, and the bucco-pharyngeal plate so formed breaks through to form the bucco-pharyngeal opening. That part of the alimentary canal that lies anterior to this opening is therefore the preoral gut, and it later breaks down and is dispersed. The fundament of the naso-hypophysial canal has in the meantime grown inward as a solid strand until it reaches the ventral surface of the infundibulum. Close to its outer end it is in contact with the dorso-posterior surface of the

button and the related evagination of the preoral gut, but it does not elsewhere come into contact with the alimentary canal.

Comparing the conditions in these embryos with those in *Petromyzon*, it is evident that the naso-hypophysial strand of *Amia* corresponds in its relations to the brain and to the bucco-pharyngeal upper lip to the prehypophysial pit of *Petromyzon* together with the hypophysial strand of that fish. The enlarged anterior end of the upper lip, which bears the adhesive organ, is generally considered to be the homologue of the anterior end of the upper lip of *Petromyzon*, which would imply that the stage of development represented in the 5-day old embryo of *Petromyzon* had been omitted in the ontogenetic development of *Amia*.

The growth forward of the bucco-pharyngeal upper lip has apparently pushed to either side the anterior ends of the premandibular tissues in which the palatine processes of the palatoquadrates develop, and these processes are directed anteriorly instead of, as in the Plagiostomi, transversely beneath the trabeculae. In connection with this a maxillary breathing valve has been developed, and it has the topographical relations to the enlarged anterior end of the bucco-pharyngeal upper lip that the tentacles of *Acipenser* have, and also the same relations to that lip that the reflexed antero-ventral edge of the upper lip of *Petromyzon* has; this suggesting that these several structures are homologous. The tentacles of *Acipenser* would then not be the homologues of the adhesive organs of the Holostei, this being as Sawadsky (1912) has, for other reasons, concluded. A maxillary breathing valve could accordingly only be present in fishes in which the bucco-pharyngeal upper lip extends forward to the end of the snout, and it has in fact not been described, so far as I can find, in any of the Plagiostomi. I formerly concluded (Allis, 1900) that it was present in rudimentary form in *Polypterus*, but this is evidently incorrect, for the naso-hypophysial canal of this fish opens in the roof of the buccal cavity, as it does in the Plagiostomi.

TELEOSTEI

In an early embryo of *Hippocampus* described by Dohrn (1881) the alimentary canal is shown extending forward slightly beyond the tip of the notochord. Beyond that point the line of the canal is continued by a band of tissue which extends forward to the anterior end of the head and is there in contact with the deeper layer of the ectoderm at the bottom of a slight depression which represents the beginning of the development of a head fold. Dohrn says that it was impossible to determine whether the cells of this line of tissue were of ectodermal, endodermal or even mesodermal origin. The hypophysis is said to develop in that part of this line that lies directly beneath the infundibulum and to be double at its origin, one part lying on either side of the median line. It is said to lie anterior to the mandibular cleft (mandibulare Spalte), the latter cleft extending upward behind the eyeball to the level of the dorsal ends of the more posterior visceral clefts.

Comparing the conditions in this embryo of *Hippocampus* with those in early embryos of *Bdellostoma*, it is evident that that part of the band-like line of tissue above described that lies anterior to the hypophysis must correspond to the prehypophysial portion of the naso-hypophysial fold of *Bdellostoma* together with that pocket-like prolongation of the fold that reaches and fuses with the anterior end of the preoral gut. The hypophysis of *Hippocampus* would then correspond to that prolongation of the pocket of *Bdellostoma* in which the hypophysis develops, and in the latter fish, as in *Hippocampus*, it is primarily double. That part of the line of tissue that lies posterior to the hypophysis would then be the preoral gut. The buccal depression and the buccopharyngeal plate are not yet indicated, for the head fold has not yet been sufficiently developed to bring the external ectoderm in contact with the ventral wall of the fore-gut. When the latter plate develops, it must lie immediately anterior to the ventral ends of the mandibular mesodermal arches, between them and the hind end of the preoral gut.

In a slightly older embryo of *Hippocampus* the ventral ends of the visceral arches are said to have shifted forward relatively to the overlying portion of the brain, the ventral ends of the mandibular arches lying near the anterior end of the embryo and considerably anterior to the hypophysis. The head fold has been somewhat deepened and extends posteriorly beyond the mandibular arches to about the middle of the ventral ends of the hyal arches. The alimentary canal is shown extending forward as a thin band-like structure to the anterior edge of the mandibular mesodermal arches. There it curves ventrally, expands somewhat, and its walls become continuous with the deeper layer of the ectoderm, that layer breaking through at this point but the external layer of the ectoderm passing over it unbroken. The hypophysis remains directly beneath the infundibulum and is there connected by a stalk with the dorsal surface of the band-like portion of the alimentary canal.

Comparing the conditions in this embryo with those in the earlier one above described, the first impression is that the anterior prolongation of the alimentary canal of the older embryo is simply an extension of the cavity of that canal in the line of tissue that I have considered to represent the preoral gut together with the naso-hypophysial fold. This is however evidently improbable, for if it were so the mouth of *Hippocampus* would correspond to the so-called primitive mouth of v. Kuppfer's description of *Bdellostoma*. It is therefore quite certain that the fore-gut has simply shifted forward to the same extent as the related portions of the visceral arches, and that the line of tissue that, in the earlier embryo described, apparently represented the preoral gut together with the naso-hypophysial fold has either been crowded forward to the anterior end of the snout, or broken down and dispersed. The buccopharyngeal plate would then lie immediately anterior to the ventral ends of the mandibular mesodermal arches, the tissue of the premandibular arches would lie anterior to this, and the conditions would be, in principle, as in the other fishes above considered. In later stages a small buccal depression

develops in the external layer of the ectoderm and when it breaks through, the definitive bucco-pharyngeal opening is formed.

In a 49-day old embryo of *Salmo salar* described by Lundborg (1894) the brain is shown prolonged anteriorly considerably beyond the notochord, and a deep head fold extends posteriorly beneath it and meets and fuses with what has the appearance of being the anterior wall of the alimentary canal, but is certainly, as in the other fishes above considered, the anterior portion of the ventral surface of the fore-gut. The plate so formed extends from below dorso-posteriorly, instead of dorso-anteriorly, and is called by Lundborg the lower jaw, but it is certainly the bucco-pharyngeal plate and is so designated (Rachenhaut) by B. Haller, as described immediately below. The long dorsal wall of the head fold later becomes the roof of the buccal cavity, and slightly anterior to the bucco-pharyngeal plate, and directly beneath the infundibulum, two pocket-like invaginations of the deeper layer of the ectoderm are said by Lundborg to develop, one on either side of the median line and close to it. The external layer of the ectoderm is said to later break through, the cavities of the two pockets then opening directly to the exterior. These two invaginations then fuse with each other and form the hypophysis, the ectoderm becomes continuous beneath it, and the hypophysis is connected with the deeper layer of the ectoderm by a solid stalk which later breaks down and becomes dispersed. No preoral gut is either described or shown in the figures, but a line of scattered cells is said to extend forward from the hypophysis, thus corresponding to what I have considered to be the naso-hypophysial fold of Dohrn's descriptions of his earliest embryo of *Hippocampus*.

In a 4 mm. embryo of *Salmo irideus* B. Haller (1896) describes a head fold similar to that in *Salmo salar*, and the hind end of the fold, where it abuts against and fuses with the wall of the alimentary canal, is called by him the Rachenhaut (bucco-pharyngeal plate). The hypophysis is said to first appear as a thickening of the ectoderm that forms the dorsal wall of the head fold, at a point slightly anterior to the dorsal edge of the bucco-pharyngeal plate, but it soon separates completely from that ectoderm excepting where a short and solid stalk connects the two. No invagination of the ectoderm is described, the latter always remaining even and unbroken. A short diverticulum is said to extend forward from the dorsal wall of the alimentary canal immediately posterior to the dorsal end of the bucco-pharyngeal plate and to closely approach both the hypophysis and the infundibulum, but not to come into contact with either of them.

Dohrn says that in the Teleostei examined by him the mandibular clefts first broke through laterally and that these two openings were extended ventrally until they met and fused with each other in the median line; and Platt (1891) describes similar conditions in *Batrachus tau*. Lundborg, however, did not find these lateral openings of the clefts in any of the Teleostei examined by him, and he thinks that those described by Dohrn were artifacts due to the reagents used. If the walls of the mandibular visceral pouches take some part

in the formation of the bucco-pharyngeal plate, as seems quite probable, there would be nothing improbable in the plate breaking through at its lateral edges before it did in the median line.

There is in the Teleostei, as in *Amia*, a maxillary breathing valve and, as also in the latter fish, the palatine processes of the palatoquadrates are directed anteriorly instead of transversely beneath the trabeculae.

Comparing the conditions in these fishes with those in the other fishes above considered, it seems practically certain that there was primarily in them, as in *Acipenser* and *Amia*, a naso-hypophysial canal or strand, and that its development has simply been slurred over or completely suppressed in ontogeny. The connection of the hypophysis with the dorsal wall of the alimentary canal of *Hippocampus* and with the dorsal wall of the buccal cavity in *Salmo* would then be of secondary origin.

SUMMARY AND CONCLUSIONS

The hypophysis develops in the deeper part of what is primarily either an open fold of the external ectoderm (Plagiostomi), a pocket-like extension of such an open fold (*Bdellostoma*), or a pocket or solid strand that arises as an infolding or ingrowth of the deeper layer only of the ectoderm, the external layer of the ectoderm passing over it unbroken (*Petromyzon*, *Acipenser*, Teleostomi). The hypophysis never arises, in any of the fishes here considered, in relation to a simple pit-like invagination of both layers of the ectoderm.

This fold, pocket or strand may be called the naso-hypophysial. It extends, when fully developed, from the lobus olfactorius impar (neuropore) to the hind end of the infundibulum, and lies, throughout its entire extent, in close proximity to that part of the cranial wall. It never extends posteriorly beyond the infundibulum and may be said to present two regions, a hypophysial and prehypophysial, the line between the two lying somewhere in the region between the recessus preopticus and the anterior end of the infundibular depression. The hypophysial portion, when it reaches the ventral surface of the infundibulum, there receives a nervous strand that grows outward from the latter.

The dorsal wall of the deeper portion of the fold, pocket or strand always lies, in all of the fishes considered, immediately beneath the ventral surface of the infundibulum.

The morphologically ventral surface of the deeper portion of the fold, as found in the Plagiostomi, lies against the ventral surface of the preoral portion of the alimentary canal. This type of fold and the related hypophysial pit (Rathke's pocket) are only developed when, in early embryonic stages, the head is lifted sufficiently above the dorsal surface of the egg to permit the swinging downward and backward of the anterior surface of the brain around the anterior end of the preoral gut. There is never, in any of the Plagiostomi here considered, any communication between the cavities of the fold and the canal. An apparently secondary and indirect communication is, however, said to

occur in *Torpedo*, where there is a pair of so-called proboscis pores, each of which extends from Rathke's pocket to the premandibular head cavity of its side.

The conditions in early embryos of the Crossopterygii are not known. In all of the other non-elasmobranchian fishes considered the head is not sufficiently lifted above the dorsal surface of the egg in early embryonic stages to permit the swinging downward and backward of the infundibulum around the anterior end of the alimentary canal, and furthermore the infundibulum does not shift forward beyond the anterior end of the canal. The ventral surface of the deeper portion of the hypophysial pocket or strand of these fishes accordingly lies actually or morphologically dorsal to the preoral gut and the cavities of the pocket and gut may be, at certain stages of development, directly continuous with each other (*Bdellostoma, Acipenser*).

The tip of the hypophysial fold, pocket or strand apparently always lies at the point where the cranial and visceral ectoderms meet and are continuous with each other.

The prehypophysial portion of the naso-hypophysial fold is always either completely fused with the dorsal surface of the related portion of the head fold, or separated from that fold by the bucco-pharyngeal upper lip which is, in the Cyclostomata, of secondary origin. In the Chondrostei and Teleostomi this lip is found *in situ* in the earliest embryos described.

Considering the conditions in these several fishes the suggestion is evident that there was primarily a visceral cleft in the median line between the premandibular arches of opposite sides, and whether there were one or more of these premandibular arches is unimportant in so far as this is concerned. This unpaired premandibular cleft is later reduced and finally suppressed as a result of the development of the fore-brain and the related descent of the infundibulum. A bucco-pharyngeal opening is then developed in the floor of the alimentary canal between the ventral ends of the mandibular and premandibular mesodermal arches, the hypophysis developing in some relation to the premandibular cleft.

The polar cartilage of either side is the pharyngeal element of the related mandibular arch, the trabecula and the palatine process of the palatoquadrate apparently being, respectively, the entire dorsal and ventral halves of the premandibular arch.

The descent of the infundibulum compresses the underlying premandibular (preoral) portion of the alimentary canal and causes its ultimate breakdown and dispersion. As a result of this, the related portion of the notochord is greatly reduced or completely suppressed, and the dorsal end of the premandibular arch (trabecula) loses its connection with the axial skeleton and acquires connection with the distal end of the polar cartilage (pharyngo-mandibula).

When in early embryos the anterior portion of the head is embedded in the dorsal surface of the egg, the polar cartilage fuses with the anterior end of the related parachordal, but when the head is raised above the surface of the egg

and prolonged anteriorly beyond it, the polar cartilage fuses with the ventral surface of the parachordal.

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THE OCCURRENCE OF A TENUISSIMUS MUSCLE IN A HUMAN ADULT

By H. L. H. H. GREEN
Demonstrator of Anatomy in the University of Cambridge

THE muscular anomaly which is to be described is as interesting as it is rare. I have been able to find only one other similar case recorded and this was by Wood (14) in 1867. His case was so similar that the diagram which he reproduced in his paper would have been adequate as an illustration for the present paper except that the all-important nerve supply was not shown, nor was it mentioned in the text.

DESCRIPTION OF SPECIMEN

The muscle (Fig. 1) was discovered during the routine dissection of a muscular male subject, aged 64 years. The condition was unilateral. In the back of the right thigh a fusiform muscle, flattened antero-posteriorly, was found emerging from under cover of the gluteus maximus and joining the biceps femoris at the junction of its long and short heads. On reflecting the gluteus maximus the muscle was seen to arise by means of a flattened and expanded aponeurosis from the fascia covering the deep aspect of the gluteus maximus. The aponeurosis faded into the fascia and could not be traced to the sacrum or coccyx though it was pointing in the direction of these structures. Followed distally, this aponeurosis quickly changed to a flat tendon a little over 1/10 inch wide, and this in turn to the muscle itself which was $\frac{1}{2}$ inch wide. The upper tendon and aponeurosis were together $3\frac{1}{2}$ inches long; the muscle belly $6\frac{1}{2}$ inches. The latter narrowed slightly at its distal end and contained a few tendinous fibres. It was inserted at the junction of the two heads of the biceps femoris, with perhaps a rather more intimate attachment to the long head of that muscle.

The tibial and the common peroneal nerves were separated from each other throughout their course in the thigh.

The nerve supplying the muscle entered its substance about half way along its length and arose from the common peroneal nerve in common with the nerve supplying the short head of the biceps femoris.

Throughout its length the muscle was placed posterior (ventral) to the common peroneal and to the tibial nerves.

DISCUSSION

From its form, position, origin, insertion and in particular from its nerve supply, there is little doubt that this anomalous muscle is a persistent tenuissimus. Though in the majority of those Mammals which possess a tenuissimus it arises from the coccyx, its origin from the gluteal fascia in this specimen is

very similar to the origin of the tenuissimus in many platyrrhine monkeys (Klaatsch).

There appears to be only one other homology which might be considered possible for this muscle: since it is supplied by a branch (nervus ischiadicus dorsalis of Appleton) from the common peroneal nerve, it might be held to represent a M. femorococcygeus (Leche).

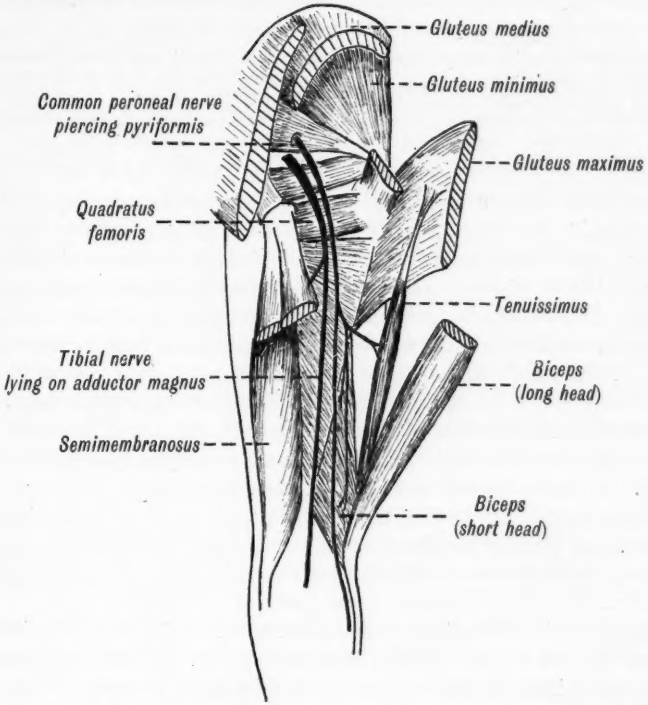

Fig. 1. Diagram of the posterior aspect of the right thigh to show the position and the nerve supply of the M. tenuissimus. The gluteus maximus and the long head of the biceps femoris are represented as cut and turned laterally.

Windle and Parsons (13), and later Klaatsch (7), showed that the short head of biceps is probably derived from the tenuissimus muscle: this view has recently been further supported by Appleton (1) on the grounds of the relations of the cutaneous nerves, despite the admittedly different relation of the two muscles to the common peroneal nerve. It is interesting to notice in this connection that the two heads of the biceps may be completely dissociated from each other in Man as in the case described by Hepburn (6).

Now the principal distinguishing features between the tenuissimus and the femorococcygeus consist in the sites of distal attachment (to the fibula and

to the femur respectively) and in the relation of these attachments to the common peroneal nerve, which passes between them. Both are supplied by the N. ischiadicus dorsalis, but the nerve to femorococcygeus is commonly associated with that for the gluteus maximus, whereas that for the tenuissimus usually arises more distally from the common peroneal nerve.

In the derivation of the short head of biceps from a tenuissimus and from a femorococcygeus the following respective changes would be involved:

Tenuissimus	*Femorococcygeus*
1. The origin migrating from the caudal vertebrae to the shaft of the femur.	1. The origin migrating from the caudal vertebrae to the shaft of the femur.
2. The insertion migrating proximally along the shaft of the fibula and its consequent displacement proximal to the common peroneal nerve.	2. The insertion migrating distally from the femur to the head of the fibula.

There is no indication that the femorococcygeus has ever been attached to the fibula in the forerunners of Man. Gadow(4) and Leche(8) derived the femorococcygeus from the M. extensor ilio-tibialis, in which case it would have had a primitively distal attachment. Appleton(1), however, has shown that, despite the fact that in many Mammals (e.g. in many Macropodidae, Rodents, Ruminants, Carnivores and Insectivores) the attachment of the femorococcygeus is on the patella and distal end of the femur, this is probably not the primitive condition. He favours a primitive attachment for the gluteus superficialis to the neighbourhood of the third trochanter, the femorococcygeus being secondarily split off from this gluteus superficialis sheet and migrating distally. He further believes(2) that in Man the femorococcygeus is represented by a part of the lateral intermuscular septum, thus continuing the insertion of the gluteus maximus down the femoral shaft. If, therefore, the short head of biceps were a derivative of the femorococcygeus, a displacement of insertion from femur to fibula must have been involved.

There seem to be no intermediate conditions suggesting a derivation of the short head of biceps from the femorococcygeus. In fact, the two muscles co-exist quite independently of each other in some Mammals. A glance at Appleton's(1) figure of the gorilla (fig. 10, *C*, page 402), in which both the muscles are present, is sufficient to convince one that the short head of biceps could not be derived from the femorococcygeus.

On the other hand, there seems to be convincing evidence in favour of the tenuissimus having become the short head of biceps as shown by Windle and Parsons' work on the edentate hind-limb, by Klaatsch's observations, and by Appleton's investigations into the relations of the cutaneous nerves in this region.

Windle and Parsons arrived at their conclusions chiefly on the grounds that they had never found a tenuissimus and a short head of biceps co-existing in the same limb: the two muscles seemed to be mutually exclusive. Though both muscles are present in the case I have described, far from invalidating the theory put forward by Windle and Parsons, substantial support is offered.

The abnormal muscle may be considered as a piece of tenuissimus which has been left behind in the "muscle-slide" which these authors visualised: "...the intermediate condition described in *Myrmecophaga*, where the caudo-femoralis muscle is apparently acting as a 'muscle-slide' down which the tenuissimus is creeping to its lower attachment." (Parsons used the name caudo-femoralis for the muscle which Leche called femorococcygeus.)

Any objection to deriving the short head of biceps from the tenuissimus on account of the difference in the relations of the common peroneal nerve to the insertions of these muscles can be overcome when it is remembered that the insertion of the long head of biceps has admittedly migrated across the common peroneal nerve in human phylogeny. Tenuissimus acts to some extent synergically with the biceps and a similar migration would seem not only possible but probable. The tenuissimus in the case described above illustrates an actual instance of such migration since it is there inserted, in common with the biceps, proximal to the nerve.

Fig. 2 will help to show the variability of the insertions of tenuissimus and biceps to the common peroneal nerve. In *Cebus*, a tenuissimus is present and is inserted half-way down the shaft of the fibula, considerably distal to the common peroneal nerve which emerges under cover of the expanded aponeurosis of insertion of the long head of biceps. In *Ateles* there is no tenuissimus but there is an extensive short head of biceps which is inserted proximally into the fascia over the lateral side of the knee and the upper part of the leg, while distally it is inserted directly into the shaft of the fibula: the common peroneal nerve crosses the bone just above this fibular attachment. *Ateles*, therefore, has a short head of biceps which is inserted both proximal and distal to the common peroneal nerve. In the human anomaly described the tenuissimus and the short head of biceps are inserted entirely proximal to the common peroneal nerve.

Lastly, although the extent of union of nerve bundles is by no means constant, there is a certain conservatism even in this, and the fact that the nerve supply to the short head of biceps and to the additional muscle (tenuissimus) arose by a common trunk from the common peroneal nerve is in favour of the two muscles having a common origin.

The occurrence of a distinct tenuissimus muscle in Man must be a very rare phenomenon. As stated above, I have been able to find only one other clear case described (Wood). This is the more extraordinary since such a muscle is hardly likely to be missed in even the most casual dissection. Wood, though recognising the resemblance of the muscle he described to the tenuissimus of the dog, thought that the latter muscle was homologous with the "caudal and sacral origin of biceps in the Rodents, and other Mammalia." This has been shown by Appleton not to be the case, the so-called caudal origin of biceps being, in some of these animals, the flexor cruris caput dorsale (Appleton), in which case it would be supplied by the tibial nerve, and in others the M. femorococcygeus of Leche.

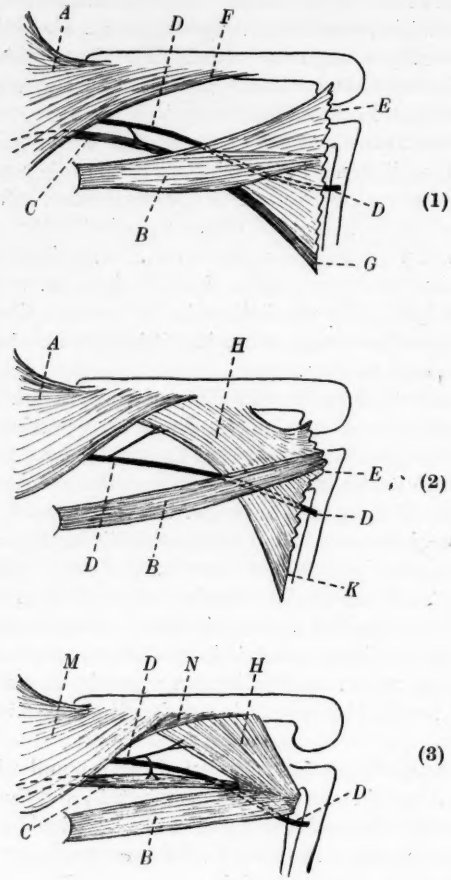

Fig. 2. Three diagrams of the lateral aspect of the thigh to illustrate the conditions found in (1) *Cebus* (sp.?), (2) *Ateles* (sp.?) and (3) the human adult described in the text.

The variation in the relation of the insertions of biceps and tenuissimus to the common peroneal nerve should be particularly noticed. The nerve supply of the tenuissimus and of the short head of biceps is shown in each case.

A. Gluteus superficialis. *B*. Long head of biceps. *C*. Tenuissimus. *D*. Common peroneal nerve. *E*. Fascial insertion of biceps. *F*. Femorococcygeus portion of the gluteus superficialis sheet. *G*. Fibular insertion of tenuissimus. *H*. Short head of biceps. *K*. Fibular insertion of the short head of biceps. *M*. Gluteus maximus. *N*. Lateral intermuscular septum representing a degenerated femorococcygeus muscle.

Several instances of additional heads to the biceps femoris in Man have been described, but from the point of view of comparative morphology the descriptions have not much interest as in none of them is the nerve supply given. The long head of the biceps may have an accessory origin from the tuber ischii (Soemmerring (11), Gantzer (5) and Blandin (3)), from the sacrum (Macalister (10)), or from the coccyx (Testut (12) and Le Double (9)). Since no nerve supply was stated it is impossible to say whether these accessory heads represented portions of a M. flexor cruris caput dorsale (Appleton), of a M. tenuissimus, of a M. femorococcygeus (Leche), or even of a M. caudofemoralis (Leche).

I am indebted to Dr Appleton for his help in the preparation of this paper, and also for lending me specimens of *Cebus* and *Ateles* for dissection.

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THE MENSTRUAL CYCLE OF THE PRIMATES

PART II. SOME EFFECTS OF OESTRIN ON BABOONS AND MACAQUES

By A. S. PARKES (*Beit Memorial Research Fellow*)
AND S. ZUCKERMAN (*Demonstrator in Anatomy*)

From the Department of Physiology and Biochemistry, and the Department of Anatomy and Embryology, University College, London

I. INTRODUCTION

A GENERAL account of the oestrous cycle of Primates, together with a detailed survey of the literature, has already been given in Part I by one of us (Z.) (4). It was there suggested that the enormous vulval and peri-anal swelling that characterises the earlier half of the baboon menstrual cycle is due to the follicular hormone. This conclusion was reached by studying these external changes in relation to the ovarian cycle, and in consideration of the fact that the sexual skin of *Macaca mulatta* (= *Macacus rhesus*) is activated by oestrin. Attention was also drawn to the remarkable cervix of *Macaca radiata* (= *Macacus sinicus*), the bonnet monkey, and its profuse mucous secretion. Four animals belonging to this species were discussed. In only one of these did it seem that there was any cyclical variation in the amount of mucus secreted. In this monkey the secretion was most profuse towards the middle of the cycle, diminishing as the menses approached. In two of the others the mucus was always profuse, while in the fourth the amount fluctuated from day to day.

The experiments described in this paper are concerned with the following problems:

(*a*) Could the enormous vulval and peri-anal swelling of the follicular phase of the baboon cycle be reproduced in an ovariectomised animal by administration of oestrin?

(*b*) Is the mucous secretion of the bonnet monkey an effect of the activity of oestrin?

(*c*) Has oestrin any effect on the sexual skin of the male rhesus macaque (*Macaca mulatta*)?

(*d*) What degree of growth of the mammary glands can be produced in monkeys by the injection of oestrin?

The latter problem is of importance in view of the statements of many authors, particularly Allen (1) in reference to Primates, that the development of the mammary glands during pregnancy is determined by the action of oestrin.

II. MATERIAL AND TECHNIQUE

The experiments were carried out on one female *Papio hamadryas*, one female *Macaca radiata* (bonnet monkey) and one male *Macaca mulatta* (rhesus monkey)[1]. In addition, an adequate supply of control material was available. The two females were ovariectomised by the ordinary surgical methods. In the baboon one ovary and a segment of the uterus were removed at a first operation, and subsequently the remaining ovary and the rest of the uterus were removed. This method was used in order to obtain material in two different stages of the cycle from the same animal, though it had, of course, the objection that the effect of the administration of oestrin on the uterus could not be observed. In anaesthetising the animals, it was found most satisfactory to give a preliminary dose of morphine and atropine, followed by ether.

After the operations the animals were left until the sexual skin of the baboon showed no signs of further atrophy, and until the flow of mucus in the bonnet macaque had stopped. Aqueous preparations of oestrin were injected subcutaneously, the dose gradually being increased until definite changes appeared.

The male rhesus, an adult, was castrated before injection.

Source of oestrin. The oestrin was prepared from urine of pregnancy by methods elsewhere described by Marrian (2). Three different batches were used, containing respectively 100, 600 and 1800 m.u. per c.c. Owing to the impracticability of giving the daily amount in a series of small injections, as is preferable with smaller animals, an attempt was made to slow down the rate of absorption of the aqueous oestrin by administration in oily emulsions. It was found, however, that a given dose produced no greater effect by this method.

Examination of mammary glands. The mammary glands were stripped off from the skin and pectoral muscle, stretched, fixed, stained in borax carmine, differentiated in acid alcohol, dehydrated, and cleared and mounted for examination in Canada balsam. Little difficulty was experienced in removing one gland at an operation ("mammectomy").

III. EXPERIMENTAL RESULTS

The histories of the three animals injected with oestrin are given below (see also p. 720, Part I(4)).

Papio hamadryas. The female baboon was experiencing normal cycles in the 4 months preceding operation.

[1] As mentioned in Part I(4), Flower's nomenclature will be used throughout.

Table I. *Effect of oestrin on ovariectomised* Papio hamadryas

Days	Operation	Oestrin per day (m.u.)	State of sexual skin	Notes
1	Right ovariectomy, partial hysterectomy	—	Down to resting level	Corpus luteum in right ovary
2–71	—	—	Cycle normal	—
72	Left ovariectomy, complete hysterectomy	—	Nearly full up	Mature follicle in left ovary
73–90	—	—	Gradual atrophy to below resting level	—
91–96	—	1,000	Gradual swelling to $\frac{1}{4}$	—
97–107	—	2,000	Some increase in swelling	—
108–117	—	6,000	Further swelling to $\frac{1}{2}$	—
118–121	—	18,000	Swelling fully up by 120th day	—
122	Left mammectomy, wedge of pudendal swelling removed	—	Swelling full	Histology of swelling normal. Left mamma as in normal oestrus
123–126	—	—	Rapid atrophy of swelling	—
127–153	—	—	Down to ovariectomy level	—
154	Autopsy	—	" "	Mammary gland somewhat atrophied

From this history, and from Plate I, figs. 1–6, the following conclusions may be drawn:

(*a*) Unilateral ovariectomy does not affect the occurrence or periodicity of the cycle in the external genitalia.

(*b*) Complete ovariectomy is followed by atrophy of the sexual skin below the resting level of the normal cycle.

(*c*) Very large amounts of oestrin are required to induce complete oestrous swelling in the sexual skin after double ovariectomy. If the baboon unit be defined as the amount of oestrin required to induce complete swelling in the time taken in the normal animal, then 1 baboon unit equals about 60,000–80,000 m.u. This is strictly comparable, on a weight for weight basis, with the amount required to cause the uterine reaction in the mouse[1]. On a similar basis, the human unit would be about 300,000–400,000 m.u. as assayed by the cornification test.

(*d*) In normal control material the mammary gland does not show any very definite changes during the ordinary cycle in the non-pregnant animal. Similarly, the development caused by oestrin after ovariectomy was apparently slight, though more than found at autopsy.

(*e*) The nature of the swelling induced by oestrin appears to be identical with that of the normal swelling.

(*f*) After cessation of oestrin injection the induced swelling subsides in about the normal time.

[1] In the mouse about 200 vaginal cornification units are required to cause the uterine reaction (3). 400 mice at 25 gm. each = 1 baboon at 10 kg.; 5 baboons (or 2000 mice) = 1 woman at 50 kg. $200 \times 400 \times 5 = 80{,}000 \times 5 = 400{,}000$.

Macaca radiata. The female bonnet monkey was in the laboratory for some 8 months before operation, but no definite cycle was observed. The copious flow of mucus from the vagina which characterises this species varied slightly in amount from time to time, but without regular periodicity.

Table II. *Effect of oestrin on* Macaca radiata

Days	Operation	Oestrin per day (m.u.)	Mucus	Notes
1	Complete ovariectomy. Sub-total hysterectomy	—	Plentiful	Neither ovary showed signs of recent activity
2–19	—	—	Gradual cessation of flow	—
20–44	—	500	Plentiful	—
45–51	—	3000	„	—
52–55	—	3600	Very plentiful	No change in sexual skin
56	Left mammectomy	—	„	Mammary gland, see Plate II, fig. 1
57–62	—	—	Gradual cessation of flow	—
63	Autopsy	—	Flow stopped	Mammary gland, see Plate II, fig. 2

From this history the following conclusions may be drawn:

(*a*) Ovariectomy of *M. radiata* stops the characteristic mucous discharge.

(*b*) Administration of oestrin causes the reappearance of the mucous flow, which ceases again after injections are stopped.

(*c*) Comparatively little difference is found between the mammary gland during oestrin injection and that taken sufficiently long after the last injection to allow of ovariectomy atrophy.

(*d*) No obvious changes in the sex skin were observed as the result of oestrin injection. This is clearly correlated with the comparative absence of cyclic change in the normal non-pregnant animal.

Macaca mulatta. An adult male rhesus monkey was castrated and injected with oestrin to ascertain whether (*a*) development of the mammary glands could be induced, and (*b*) whether changes in the pudendal skin could be induced analogous with those found in the female. 43,250 m.u. of oestrin were given over 8 days, beginning 6 days after the operation. A very slight development of the mammary gland was produced (Plate II, fig. 3), but no changes could be observed in the pudendal skin. The area in the male comparable with the sexual skin of the female is therefore markedly different in being insensitive to the action of oestrin.

We are greatly indebted to Prof. C. Lovatt Evans, F.R.S., for facilities for keeping monkeys, while our thanks are due to Prof. J. P. Hill, F.R.S., for his critical interest in the work. Certain of the operations were carried out by Mr L. W. G. Williams, to whom we would offer our best thanks. Injections and other operations were carried out by A. S. P. The oestrin was most generously provided by Mr G. F. Marrian.

Dr Fish and Prof. Hindle have very kindly provided some of the animals used.

IV. SUMMARY

1. Ovariectomy causes (*a*) immediate atrophy of the sexual skin of the hamadryas baboon, and (*b*) cessation of the flow of mucus in the bonnet monkey.

2. Injection of oestrin after ovariectomy causes (*a*) the appearance in the baboon of a swelling precisely similar to that found in the normal animal during the follicular phase, and (*b*) return of the mucous flow in the bonnet monkey.

3. Injection of oestrin after gonadectomy has no effect on the sexual skin of the bonnet monkey or on the pudendal skin of the male rhesus, and very little effect on the mammary glands of the baboon, the bonnet monkey or the male rhesus monkey.

4. The amount of oestrin required to induce the complete oestrous swelling of the baboon is about 60,000–80,000 m.u. This amount is comparable on a weight for weight basis with the amount required to produce uterine oestrus in the mouse. On a similar basis, the amount required to produce "oestrous" changes in a woman would be nearly half a million mouse units.

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DESCRIPTION OF PLATES

Plate I

Fig. 1. Ovariectomised baboon, receiving oestrin (see Table I), showing full development of the follicular swelling.

Fig. 2. Ovariectomised baboon, 31 days after last injection of oestrin, showing state of sexual skin after ovariectomy.

Fig. 3. Section through sexual skin of normal hamadryas baboon at height of swelling. × 200.

Fig. 4. Section through sexual skin of ovariectomised hamadryas baboon with swelling induced by oestrin. Swelling histologically normal. × 200.

Fig. 5. Section through sexual skin after ovariectomy, showing atrophy. × 200.

Fig. 6. As Fig. 1.

Plate II

Fig. 1. Left mammary gland of *M. radiata* receiving oestrin (see Table II). Some development in excess of Fig. 2. × ½.

Fig. 2. Right mammary gland of *M. radiata* 32 days after last injection of oestrin, showing extent of ovariectomy atrophy. × ½.

Fig. 3. Mammae of castrated male rhesus receiving 43,200 m.u. of oestrin in 8 days. Slight growth in excess of that of normal male. × ½.

Fig. 4. Mammary gland of normal baboon at climax of swelling, i.e. at time of ovulation. × ½.

The photomicrographs are the work of Mr F. J. Pittock.

Fig. 1

Fig. 2

Fig. 5

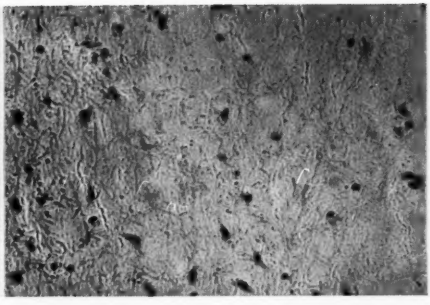

Fig. 3

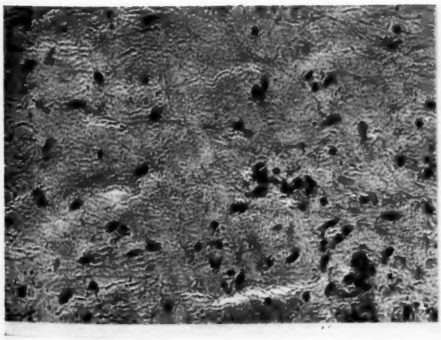

Fig. 4

Fig. 6

PARKES AND ZUCKERMAN—THE MENSTRUAL CYCLE OF BABOONS AND MACAQUES

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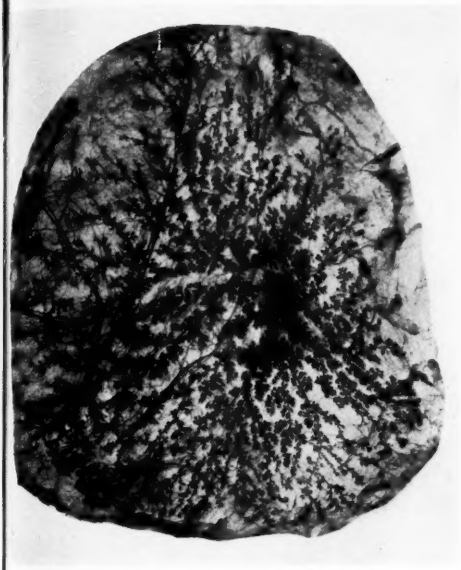

Fig. 1

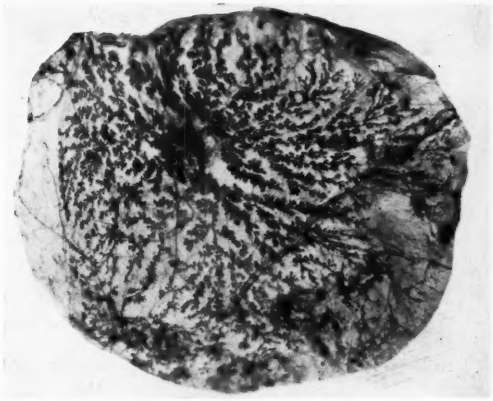

Fig 2

Fig. 3

Fig. 4

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REVIEWS

The Origin of the Human Skeleton. An Introduction to Human Osteology. By ROBERT BROOM, D.Sc., F.R.S. (London: Witherby.) 1930. Pp. 164. 2 pls., 46 figs. 10*s.* 6*d.* net.

Dr Robert Broom by writing this book has done a great service to anatomists. For over thirty years he has been collecting and studying the fossil bones of the mammal-like reptiles of South Africa, searching amongst them for the forerunners of the true mammals. The results of his original investigations have been published as contributions to learned societies; he is the author of at least 250 papers. In this book he brings together his chief results—so far as they bear on the structure of man's skeleton, and weaves them, with the help of simple drawings, into narrative form. Perhaps the title might have represented the contents of his book more truthfully if it had been changed to "The Origin of the *Mammalian* Skeleton," for the author has much to say concerning the osteology of the monotremes, marsupials and other mammalian orders besides that to which man belongs.

In this work readers will find a clear synopsis of the many researches Dr Broom has made on the transformation of the reptilian into the mammalian palate. It would be too much, perhaps, to accept all he has to say concerning the homologies of the bones of the mammalian palate, orbit, nose, jaws and face as fully proved, but as the evidence stands his identifications seem to come nearest to the truth. All parts of the skull and skeleton come under review and there is not a structure touched upon in vain; to the history of every part Dr Broom has something new to add. Sometimes he brushes aside evidence against his conclusions with undue consideration. For instance his studies of the tarsus of South African mammal-like reptiles has led him to the conclusion that the astragalus of man represents the *intermedium* and that the *tibiale* has somehow been pushed forwards to become the navicular bone of the human foot—whereas the relations of this bone in the tarsus is that of a *centrale*. Attached to the human astragalus is a small element—sometimes a separate bone—the *os trigonum*—which certainly is situated where the *intermedium* ought to be. This element Dr Broom does not consider. He rejects the idea of an original cartilaginous element (the precoracoid) being included in the human clavicle. Yet Professor Fawcett has demonstrated very definitely that there are two cartilaginous elements included in the developing human clavicle. These elements have to be explained. It is quite true that embryological processes have to be interpreted on the evidence of palaeontology and of comparative anatomy and in this particular case neither of the subjects are in a position to offer conclusive evidence. These are minor criticisms and are intended in no way to detract from the rich harvest of facts which Dr Broom has placed at the disposal of human anatomists.

Especially do we commend the line drawings given of skulls, skeletons and bones of the transitional reptilian types investigated by the author. They serve to elucidate his text. Especially welcome are two large diagrammatic charts. In one of them Dr Broom gives his conception of the inter-relationship of the various reptilian forms found in the Permian, Triassic and Jurassic rocks of South Africa, with his conception of the evolution of the mammalian orders from a reptilian stock during cretaceous and tertiary times. The reader will find it advantageous to keep his eye on this chart for the better understanding of Dr Broom's text. In the second chart he gives a family tree of the primates. All are represented as side branches of a great central stem which culminates in the human races of to-day. It is an anthropomorphic rather than an anatomical way of representing the facts. The author's idea seems to be that

the whole evolutionary movement which gave rise to the primates had as its central theme the production of man. If we are influenced by the anatomical evidence we must conclude that man is the most aberrant of all primates; in the same kind of aberrancy the anthropoid apes stand next to man. Tarsius is just as eccentric on the other side of the phylum. Far from being the central theme man is a side issue—a very surprising and important one nevertheless in any anatomical scheme—not the central one.

The Development of Sex in Vertebrates. By F. W. Rogers Brambell. Text-books of Animal Biology. (London: Sidgwick and Jackson, Ltd.) 1903. Pp. xvi + 261. 49 figs. Price 12*s.* net.

This addition to the series of text-books under the general editorship of Prof. Julian S. Huxley by a distinguished worker in one of the most fruitful fields of recent research is a valuable guide to the senior student and to the research worker in the embryology, physiology and histology of the sex glands. Spermatogenesis and öogenesis are described in detail as an introduction to the study of the sex chromosomes and the sex ratio. The origin of the primordial germ cells and the differentiation of sex is followed by a sound account of the present position as regards the function of the Graafian follicle and corpus luteum, for this has been the most fertile field of late. A discussion of hermaphroditism and sex reversal in fish, amphibia and birds is followed by a final chapter on the evolution of the gonads and the determination of sex.

The author has maintained the integrity of the chromosome theory throughout, and the recent monograph of H. M. Evans and O. Swezy has confirmed the theory for Man, in that the male somatic cell contains definitely $46 + x + y$ chromosomes and the female somatic cell $46 + 2x$ chromosomes.

The illustrations throughout the book are useful, especially the microscopic line drawings. We miss an account of certain biochemical reactions such as those of Lillie and Manoilov. Definite changes occurring in the ovary such as atresia might be more carefully defined. Such terms as "free-martin" and "pseudo-pregnancy" might be pursued to their earlier usage for there is still much to be gained by lighting one's torch at the fires of the older biologists such as John Hunter. An anatomist would be pleased to see some description of the differences in external size and configuration of the two sexes at various ages as a result of the development of sex.

The Cerebellum. An Investigation of Recent Advances. By the Association for Research in Mental Diseases. (Baltimore: Williams and Wilkins Co.; London: Baillière, Tindall and Cox.) 1929. Pp. xxii + 649. 220 figs. Price 45*s.* net.

This is the sixth of the series of monographs published by the American Association for Research in Nervous and Mental Diseases, under the joint editorship of Frederick Tilney, Thomas K. Davies and Henry Riley. The first chapter, by Dr Strong, is devoted to unsolved problems suggested by the present state of our knowledge of the cerebellar histology and fibre tracts. Our knowledge is deficient mainly as regards the afferent paths to the cerebellum, topographic representation and neocerebellar connections.

A comparative study of the arbor vitae and folial pattern in mammals by Henry Riley indicates the gradual reduction of the paraflocculus throughout the primate series. No definite conclusions are drawn as regards localisation in the anterior lobe,

but the posterior lobe can be analysed in terms of skilled movements and the unilateral independence of the fore and hind limbs. However, Ferrier's experiments relating to anterior, posterior and lateral movements are not mentioned.

Hausman deals with the morphology of the vermis, cerebellar nuclei and vestibular mass. The vestibular nuclei constitute the segmental foundation, and the subsequent evolution of the cerebellum is determined by the spino-cerebellar and cortico-pontine systems. The account of the structure and development of the proprioceptors by Elwin is based largely on the recent comprehensive work of Tello, and includes considerable embryological detail. Byrnes deals with the comparative morphology of the proprioceptors or "locomotorceptors," and indicates that the muscle spindle, absent in the tailed amphibia, is not essential to cerebellar activity in the lower animals. The membranous labyrinth and lateral line organs are traced through various forms by Larsell. Addison emphasises the four main afferent tracts in mammals, viz. from the spinal cord, from the inferior olive, from the vestibular nuclei and from the cerebral cortex by way of the pontine nuclei. Throughout the vertebrate series the main addition occurs in mammals, as the cortico-ponto-cerebellar pathway. Weil, dealing with the spinal cord, points out the preponderance of cerebellar afferents in ungulates and of cerebral afferents in the higher primates. Spino-cerebellar afferents remain relatively constant in mammals, but spino-cerebral afferents and cerebro-spinal efferents increase with mammalian ascendance. Ramsay Hunt discusses the cerebellum as an organ for the regulation of the static and dynamic equilibrium of the body masses. Frederick Miller maintains that the cerebellum contains a series of intricate reflex arcs, which, in response to streams of proprioceptive impulses from the labyrinths and muscles, emit discharges which augment or inhibit postural tone in conformity with the attitudes and movements of the body.

The localised and correlated reactions obtained by stimulation of the various folia of the cerebellar cortex in cats and monkeys are described by Mussen. Mussen claims that muscular reactions such as conjugate movements of the eyes and swallowing are definitely localised in the posterior vermis and ventral lobes respectively. The detailed report of these experiments will be awaited with interest.

The remainder of the book is devoted to certain experiments in decerebration and extirpation, to clinical studies, morbid anatomy and surgical treatment. The book as a whole is peculiarly valuable to the anatomist, physiologist and clinician. The bibliography and illustrations are excellent. The index is meagre, particularly as regards the names of workers indissolubly associated with certain landmarks in the history of the development of our knowledge of the cerebellum.

Aphasia in Children. By ALEX. W. G. EWING. (London: Oxford Medical Publications.) 1930. Pp. xi + 152. Price 10*s.* 6*d.* net.

This monograph is a record of hearing tests applied to children, largely by means of the audiometer and the "tunnel apparatus." All the tests in ordinary use are evaluated and special attention is focussed on those congenitally aphasic children who are deaf to notes of high frequency only, with an auditory range in some cases from 64 to 1024, whereas the minimum range in normal children extends from 80 to about 8000 vibrations. Many children previously classified as deaf and dumb were shown to be linguistically retarded by reason of this deafness to sounds of high frequency.

The second part of the monograph deals with the investigation of aphasic symptoms, and distinguishes between the aphasia of adults and that of children. The correlation between difficulty in reading and defective pitch discrimination, and the complete dependence for development of the speech-language function on auditory stimulation over a wide frequency range is proved. It is not determined as to whether

the seat of the defect in these retarded children is in the cochlea, along the auditory path or even due to late myelinisation of the nerve fibres.

The author, who is not a medical man, is to be congratulated on the manner in which he has discriminated between failures in natural speech development in childhood and the breakdown of the perfected processes in later life. Neurologists and educationists will appreciate the fundamental character of the work.

Repetitorium Anatomicum. By Prof. G. BROESIKE. (Second edition by Dr MAIR.) (Leipzig: Fischer's Medicinische Buchhandlung.) 1930. Pp. xi + 305. 71 figs. Price 22 marks.

This synopsis of human anatomy can be recommended to students who wish to gain familiarity with German anatomical literature as the definitions of terms and structures are particularly lucid and simple. The form of the book demands short crisp sentences in typical didactic form, and this is a great advantage to the English reader. The illustrations, particularly those of the central nervous system, are excellent and the price is within reach of the student. The book can be recommended instead of the more expensive anatomical atlases as an easy road to the acquirement of a German vocabulary.

Shorter Convalescence. By Lieut.-Colonel JAMES K. MCCONNELL. (London: Wm. Heinemann (Medical Books), Ltd.) 1930. Pp. xi + 132. Price 5*s.* net.

This short hand-book by so enthusiastic an exponent of massage and medical gymnastics as Lieut.-Colonel McConnell is a valuable summary of the main exercises which can be used to guard against loss of tone during illness, and to acquire physical fitness rapidly during convalescence. The exercises designed for the circulatory, respiratory and digestive systems are invaluable not only on the score of their sound anatomical and physiological basis, but also on the extent to which they make use of the mentality of the patient as a guard against boredom. The language is concise and the presentation affords considerable help to the nurse, student and doctor.

Aquatic Mammals. Their Adaptation to Life in the Water. By A. BRAZIER HOWELL. (Illinois: Charles C. Thomas, Springfield; London: Baillière, Tindall and Cox.) 1930. Pp. xii + 338. 45 figs. Price 22*s.* 6*d.* net.

There are signs of a revival in morphology in the schools of anatomy wherein experimental embryology has monopolised the field for many years. This book, by the comparative anatomist at the Johns Hopkins University, is an attractive attempt to depict the main aquatic specialisations. The author claims the right to put forward hypotheses and emphasises how meagre are the anatomical facts in relation to this specialised group of mammals. The modes of aquatic propulsion in aquatic mammals are compared with those in aquatic vertebrates and a brief account is given of the external features in all forms including the fossil reptiles.

The specialised features of the various species are considered in terms of visual, acoustic and olfactory adaptations, and the respiratory apparatus of the mouth and nose is discussed in detail. The vexed problem of the telescoping of the cranial axis leads to interesting theories in relation to the morphology of the skull. It is held that the form of the skull has been determined far less by flotation and water pressure than by muscle migration in relation to minimal cephalic movement. The neck, the trunk and the tail lead to an expression of views in relation to "stream-lining" and

increased resistance to the water. The pectoral and pelvic limbs are traced through numerous forms from Ornithorhynchus to the Cetacea, and the problems discussed include the loss of synovial joints, the development of hyperphalangy, and the loss of the nails.

The final chapter deals with physiological features of the cardiovascular, urogenital and respiratory systems. It is obvious that observation of the living specimens, experimentation and a study of embryological forms alone can replace the myth and fancy which now occupy so large a space in our knowledge of these forms which are so threatened with commercial extinction. The bibliography, illustrations and general format of the book are satisfactory, and there is a philosophical trend in the author which is reminiscent of the charm of the earlier writers in comparative anatomy.

Baillière's Synthetic Anatomy. By J. E. CHEESMAN. Part IV. Thigh and Hip. Part IX. Head and Neck. Part IX A. Pterygo-Maxillary Region. (London: Baillière, Tindall and Cox.) 1928–9. 12 Plates in each part. Price 3*s.* per part.

The general features and possibilities of this now familiar Atlas have been sufficiently indicated in reviews of earlier parts in the series (this *Journal*, vol. LXI, p. 386; vol. LXIV, p. 537). The section on Thigh and Hip suffers in the gluteal and popliteal regions from the small scale used. The same is true of the section on Head and Neck, but a central area including the pterygoid and submaxillary regions has been reproduced, in the third part under present consideration, on a scale greater than life size. The crowded and complicated relationships in the head and neck cannot be set out as clearly in a series of planes through the whole region as it is possible so to portray the anatomy of the limbs. Parts IX and IX A show a valiant attempt to deal with this difficult region; but the effort to interpret the plates must be equally valiant and it is doubtful if the average student will prove equal to it.

The terminal part of the lingual nerve and its relation to Wharton's duct are incompletely shown in both the small and large scale figures. The brain is not shown in the plates of the entire head, so that cranio-cerebral relationships cannot be worked out.

Introduction to Anatomy. By N. S. SAHASRABUDHE. To be obtained from the author—Sitabuldi, Nagpur, C.P., India. 1929. Pp. ix + 236. 13 plates. Price not stated.

Probably a volume meeting a long felt want in Indian schools, for which it is alone fitted. It is useful inasmuch as it attempts to induce thought and reasoning in place of the usual "parrot-method" of memorising. There are a few errors both typographical and of fact. The plates are not satisfactory.

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THE CEREBELLUM OF *SPHENODON PUNCTATUM*

By J. C. R. HINDENACH, M.B., Ch.B.
Department of Anatomy, University of Otago, New Zealand

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INTRODUCTION

The brain of *Sphenodon punctatum* has, for the past thirty years, held an important position in the field of comparative neurology, mainly due to the interest centering round the forebrain and pineal organ of this primitive reptile. Of recent years the cerebellum of man has been studied from a comparative anatomical view-point, and Dr W. P. Gowland suggested the study of the cerebellum of *Sphenodon* to me as an almost unexplored field. Up to the present no detailed account of its cerebellum has been given.

Gisi (1907) has published an exhaustive survey of certain aspects of its brain, confining herself chiefly to the external appearances and the relation of the brain to the skull. Her discussion of the internal structure of the cerebellum is incomplete. Apart from the work of Gisi, I know of no other detailed study of the cerebellum of *Sphenodon*. The greater portion of this account was therefore written on a basis of comparison with the brains of other vertebrates as described in available journals. In connection with the study of comparative neurology in New Zealand, one is hampered to some extent by the lack of some of the most important papers dealing with the reptilian brain.

At the present time, there is also a lack of suitably stained series of other reptilian brains for comparative purposes. For these reasons the following study has been made chiefly from a descriptive point of view, and a discussion of the possible homologies avoided where possible.

In addition, no detailed work has yet been done on the mesencephalon or the medulla oblongata of *Sphenodon*, and accordingly it has been difficult to link up completely the cerebellum by its connections, with the result that several of the cerebellar tracts still require further investigation.

The nomenclature used has been adopted from that in the works of Prof. C. Judson Herrick on the cerebellum of *Necturus* and other urodele amphibia,

and of O. Larsell who has written on the cerebellum of *Amblystoma*, of the frog and of certain reptiles.

In connection with this study, I wish to express my thanks and indebtedness to Prof. W. P. Gowland, head of the Department of Anatomy of the University of Otago, at whose suggestion this work was commenced, and by whose efforts, serial sections of the brain of *Sphenodon*, suitably stained by modern neurological technique, have been made available for the detailed study of its internal structure.

MATERIAL AND TECHNIQUE

For this study, numerous series of sections of the brain of the adult *Sphenodon* were employed. Several foetal brains were available, stained by Huber's toluidin blue technique, but they were not sufficiently early to draw any conclusions concerning the development of the cerebellum.

For examination of the cell masses, the toluidin blue series were used. These were stained by the method suggested by Prof. G. Carl Huber, University of Michigan, Ann Arbor, and proved of the utmost value.

The fibre tracts were examined mainly in Weigert preparations, but use was also made of the material prepared by the silver impregnation method of Cajal which allowed of the recognition of non-medullated fibres.

Other series stained by the methods of Ranson, Gurdjian and Golgi-Cox also proved of use.

The following adult material was available for study:

Stained by Huber's toluidin method: six transverse series, four sagittal series, and one horizontal series;

Stained by the Weigert method: one transverse series, one sagittal series, and two horizontal series;

Stained by Cajal method: two transverse series, two sagittal series, and two horizontal series;

Stained by Ransom method: one transverse series;

Stained by Gurdjian III method: one sagittal series;

Stained by Golgi-Cox method: one transverse series.

GENERAL

The cerebellum of *Sphenodon* is of a most primitive type, being in the usual extroverted form characteristic of reptiles. Kappers (1921) has described the similarity between this reptilian type and the developing cerebellum of the human foetus. Larsell (1926) states that de Lange (1917) has called attention to the similarity between this extroverted form and that of the early foetus, and also between the alligator type and that of the 3 months' foetus. Larsell (1926), describing the cerebellum of *Gerrhonotus principis* and *Sceloporus biseriatus*, correlates the former with that organ in the human of about three

months, and that of the latter with the 2 months' human foetal stage. The external appearance of the cerebellum of *Sphenodon* corresponds very closely to that seen in the 27 mm. (2 months) human foetus, as pictured by Kappers (1921, p. 706), and the similarity appears to be even more complete than that described above for *Sceloporus*.

It is of interest to note here the comparison made by Hines (1923), where she states that in the development of the telencephalon of *Sphenodon*, a stage is reached resembling point for point that of the 11·8 mm. (No. 1121) human embryo belonging to the Mall collection.

The degree of extroversion as seen in the series of brains of *Sphenodon* at my disposal, varies considerably. In one series (fig. 1) the cephalic surface, or molecular layer, is closely approximated to the convex surface of the optic tectum, and this is also demonstrable in longitudinal sections of the head of the embryo with the brain *in situ*. Other series show a considerable distance between the tectum and the cerebellum, the latter organ curving far caudally over the IVth ventricle from its attachment to the cephalic portion of the medulla. This variation is most probably explained by some loosening of the membraneous attachments of the cerebellum to the optic tectum during removal and fixation of the brain. I have had no opportunity of examining the brain *in situ* to determine the exact position, but I believe the former description, as present in the late embryo, is the more correct.

Another varying feature in the cerebellum is its size. The thickness of this organ and its lateral extent are comparatively constant, but its length varies to a considerable extent. In medial longitudinal sections, the length in one specimen is almost double the length in another. Whether this is due to a differentiation in type, or to a varying development of the musculature, it is impossible at present to offer any opinion.

The cerebellum can be described as being roughly of a triangular shape, the narrow base being the attached border, and the angles at the base being elongated laterally and rostrally to form the auricular lobes. This triangular sheet is concave anteriorly from base to apex, and also concave anteriorly from side to side, thus producing the typical extroverted form. In most specimens the cerebellum slopes caudally and dorsally from its attached base at about an angle of 70° with the horizontal, then passes dorsally, and finally curves rostrally to the tip. The rostral surface in these specimens is related to the optic tectum, the space between them being filled with pia-arachnoid. As I have previously mentioned, this relationship varies in different series. In sagittal sections the cerebellum is also triangular, tapering gradually from base to apex.

The bilateral origin is definitely shown by a longitudinal furrow in the midline of the caudal surface, dividing the cerebellum into two symmetrical halves. This sulcus is deepest at its commencement on the ventricular portion of the caudal surface, and gradually becomes less marked as it passes towards the tip, before reaching which, it disappears. This posterior median sulcus appears

to invaginate the cerebellum, with the result that the cerebellum in horizontal cross section appears almost W-shaped (fig. 13 A), the two legs of the W being the auricular lobes, and the median portion being due to the pushing rostrally of the posterior sulcus. On either side of the midline, there is a thickening of the mass of the cerebellum which gradually tapers to the lateral rounded borders.

The rostral limit of the cerebellum is determined medially by the decussatio veli (fig. 1). Laterally, the rostral limit is more difficult to determine. It appears to be bounded by the nucleus isthmi which makes a definite projection on the dorso-lateral surface of the isthmial region, visible to the naked eye. The nucleus isthmi, though not actually a part of the cerebellum, is closely related to it, both anatomically and by its fibre connections, and therefore will be described in this paper. As stated above, it is large in *Sphenodon* and has the IVth nerve passing over its dorsal and lateral aspects.

The angles at the base of the cerebellum are bent rostrally to form the auricular lobes, thus forming an anterior furrow between them and the body of the cerebellum; but no sulcus could be seen between the ventral portion of the auricle and the medulla oblongata.

The caudal limit of the attachment of the cerebellum to the medulla is definitely marked, and lies about the level of the entrance of the Vth cranial nerve.

HISTOLOGY

The cerebellum of *Sphenodon* consists of three typical layers. These areas correspond closely to the condition found in other reptiles and even to the zones seen in the cerebellar cortex of higher vertebrates. The layers are: a molecular layer, a layer of Purkinje cells, and a granular layer (figs. 1, 10). The relations of these layers to each other can be studied in the series available, but without further Golgi preparations I am unable to give a detailed description of the types of neurones present and their ramifications.

A well-marked fibre layer is also present, lying partly between the above zones and partly through them.

The granular layer is distinct, and consists of small, darkly stained, rounded cells closely packed together. The layer is divided into various strata by the entering fibres of the cerebellum, thus giving this zone a laminated appearance in cross section. The greatest number of cells are present near the ependymal layer.

The extroversion of the cerebellum has altered the position of the granular layer from a purely caudal one. This layer, therefore, lies on the lateral surface of the auricular lobes, the ventral or ventricular surface of the base of the cerebellum, the caudal surface of the body and the dorsal surface of the tip. The thickness of the granular layer varies but slightly in the different parts of the cerebellum. It is thickest at the corpus cerebelli where the granular layer projects ventrally into the IVth ventricle on either side of the midline. In this

position it forms two distinct eminences separated by a sulcus, the sulcus medialis posterior (fig. 11). The granular layer is thinnest opposite this sulcus, thickest on either side of the sulcus, and then is of almost constant thickness out to the lateral borders of the cerebellum.

The granular layer is separated from the Purkinje layer by a band of fibres which are mainly afferent in type. This band consists of commissural fibres running transversely and other fibres running longitudinally. The commissural fibres are mainly rostral to the longitudinal ones, being seen in their greatest extent in mid-sagittal section, where the longitudinal fibres are almost absent (figs. 15, 16). The fibres, which are of both medullated and non-medullated types, are not confined to the one area alone, but scatter throughout the three cell layers.

The Purkinje cells form a zone between the molecular and granular layers, or, more definitely, between the molecular and fibre layers, but scattered Purkinje cells are, however, found in the fibre layer. These cells are of the typical large ovoid shape, with darkly stained bodies and with dendritic processes, as seen in some Cajal sections, extending into the molecular layer. This stratum varies in thickness throughout the cerebellum, in some areas only one layer of cells, in others, four or five layers being seen. This variation may, in part, be due to the obliquity of the sections.

Purkinje cells extend laterally into the auricular lobes (fig. 13). They are especially numerous in the body of the cerebellum overlying the IVth ventricle. The relation of their axons to the nucleus cerebelli and the brachium conjunctivum as described by Larsell (1923) in the frog could not be definitely determined, though some fibres in the brachium conjunctivum appear to arise from regions in the cerebellum other than that of the nucleus cerebelli.

The molecular layer is seen lying in the rostral concavity due to the extroversion of the cerebellum. It is composed mainly of non-medullated fibres, though a few small, scattered, faintly stained, rounded cells are seen throughout its substance. Larsell (1923), describing this condition for the frog, suggests that these are only neuroglial cells. This layer is of approximately the same thickness as the granular layer, being of the greatest dimensions in the rostral part of the cerebellum, where it overlies the commissura cerebelli. Rostrally, it falls just short of the decussating fibres of the ventral spino-cerebellar tract. Owing to the extroversion of the cerebellum, this layer faces dorsally in the rostral part, and ventrally in the dorsal curved part of the cerebellum. The layer is related in general to the caudal surface of the optic tectum. It is bounded rostrally by the cerebellar commissure in the midline, and laterally by the arching fibres of the ventral spino-cerebellar tract.

NUCLEI OF THE CEREBELLAR REGION

The nucleus cerebelli

In the corpus cerebelli of *Sphenodon* there are present multipolar cells of large size, which bear a considerable resemblance to the Purkinje cells already described. These cells are slightly larger than the Purkinje cells, and stain less deeply. In the absence of Golgi preparations, it is impossible to describe them fully, or to trace out their connections. These cells lie in the lateral part of the cerebellum at its junction with the tegmentum of the bulb, but also extend medially into the cerebellum where it lies dorsal to the IVth ventricle (fig. 9). The cells are not collected into one mass but lie scattered throughout this region, about twenty being seen in cross section at one time. A few cells extend rostrally towards the commissura cerebelli, where they are separated from the nucleus isthmi which lies rostral, lateral, and ventral to them by the ventral spino-cerebellar tract and mesencephalic tract of the Vth nerve. Ventrally, the nucleus lies, from without in, on the tegmentum of the bulb, and the ependyma on the ventral surface of the cerebellum overlying the IVth ventricle (fig. 9). The most medial cells extend towards the midline between the granular layer and the fibre layer. Laterally, the cells are bounded by dorsal spino-cerebellar fibres and fibres of the vestibulo-cerebellar tract passing to the auricular lobe. Dorsally, the nucleus lies beneath the entering fibre tracts, while posteriorly, it comes into direct relation with the superior vestibular nucleus lying in the upper free border of the bulb (fig. 10). There is a direct continuity between the cells of both nuclei, and it is difficult to define an exact line of separation. The nucleus cerebelli lies in the midst of the ascending fibres of the vestibulo-cerebellar tract.

Thus the nucleus is brought into anatomical relationship with fibres carrying impulses from the spinal cord and also from the vestibular centres.

As stated above, the cell connections are not included in this description, but it is obvious in the sections that the fibres of the branchium conjunctivum pass ventrally and rostrally from this region of the cerebellum.

Larsell (1926) describes the deep nuclei of the cerebellum in certain reptiles as being present in two masses, medial and lateral, which are not sharply separated. The larger lateral part, he designates the nucleus cerebelli lateralis, and the attenuated medial division extending nearly to the midline of the cerebellum in the border zone between corpus cerebelli and the anterior medullary velum, is called the nucleus cerebelli medialis. The statement by Larsell that the brachium conjunctivum in *Anniella* takes origin from the lateral nucleus, is in agreement with the condition in *Sphenodon* in which the brachium conjunctivum appears to come from the more lateral cells of the nucleus cerebelli. Apart from this point there is no other means of dividing the nucleus cerebelli in *Sphenodon* into two masses.

Herrick (1914), in describing *Necturus*, states: "The cerebellar tissue in the floor of the lateral recess (eminentia ventralis cerebelli) gives rise to the greater

part of the feebly developed brachium conjunctivum and is therefore probably the primordium of the roof nuclei and the nucleus dentatus of the mammalian cerebellum." He further describes the neurones lying in this region, whose neurites can be followed for only a short distance, probably entering the tractus cerebello-tegmentalis and brachium conjunctivum. He suggests that these cells are "greatly reduced Purkinje neurones."

Larsell (1926) describes cells in the frog, lying in the border zone of the eminentia ventralis cerebelli between the nucleus cerebelli and the tegmentum, of large size suggesting Purkinje cells. He regards them as a more primitive cerebellar correlating apparatus than is found in the corpus cerebelli. Both these descriptions of Purkinje-like cells can be correlated with the condition seen in *Sphenodon* in which the cells described are, however, more definitely situated in the cerebellum.

Nucleus isthmi

There exists in the literature on this subject some confusion—mainly due to the varying cell masses in the brains of vertebrates to which this term has been applied. Larsell (1924) gives an admirable introduction to the subject, in which he clears up the general point of view. Previous writers have confused the nucleus isthmi and the secondary visceral nucleus. Johnston (1906) states that the ganglion isthmi of birds is of a different character to the ganglion isthmi in amphibia and fishes. Both nucleus isthmi and secondary visceral nucleus are in close anatomical relationship in the lower vertebrates, and confusion has thus arisen. In the fishes the large size of the secondary visceral nucleus overshadows the small nucleus isthmi, while in the reptiles the reverse is the case, the nucleus isthmi being a prominent feature in the isthmus of the brain, and the secondary visceral nucleus being comparatively small. Kappers (1921) has clarified the situation by homologising the nucleus isthmi of amphibia with that of the same name in reptiles and birds. He holds that, in these forms, it is homologous with the medial geniculate body of mammals. Larsell (1923, 1924) has described carefully both the nucleus isthmi and secondary visceral nucleus in the frog, and says that they must be regarded as two distinct and unrelated nuclei which topographically are closely crowded together.

Huber and Crosby (1926), for the alligator, give a detailed description of the connections of the nucleus isthmi, but make no mention of secondary visceral nucleus. They describe the nucleus isthmi as consisting of two nuclear masses, a larger lateral portion, and a smaller medial portion. Its fibre connections correspond closely to those described by Larsell (1926) for the frog.

Huber and Crosby (1929) also give a detailed description of the nucleus isthmi in the avian diencephalon, and subdivide it still further. They describe the pars principalis as an outer or superior portion, distinctly large celled, and use the terms pars principalis parvo-cellularis and pars principalis magno-cellularis for the two divisions of the nucleus isthmi in the dorsal region of the mesencephalon. They state that, associated with this pars principalis, is

another nuclear group, the nucleus semilunaris of Mesdrag, for which Craigie (1928) has suggested the name pars magno-cellularis ventralis nucleus isthmi. The cells of the parvo-cellularis portion are actually medium sized and only small in comparison with the other portion. The small-celled part disappears caudally before the large-celled, and it is medial to the nucleus semilunaris. Craigie (1928) states that the whole nucleus isthmi complex is well developed in the typical avian brain. He believes that it is really a differentiation of the anterior end of the area statica, and, having connections with the latter, with the tectum, and with the cerebellum, is probably a static or visuostatic correlating area. Its considerable size may thus be correlated with that of the cerebellum and of the whole equilibratory and flight mechanism. This theory is not borne out in *Sphenodon*, in which, though the nucleus isthmi is large, the cerebellum is comparatively simple and small, and the equilibratory mechanism probably rather simple in this comparatively sluggish reptile.

The nucleus isthmi in *Sphenodon* forms a distinct projection on the brain surface, dorso-lateral to the decussation of the IVth nerve, and lateral also to the posterior corpus quadrigeminum (fig. 11). It is the most conspicuous structure in the pre-cerebellar region of the brain, the fibres of the IVth nerve passing over its external surface (fig. 20).

It is oval in shape and can be divided into two distinct nuclear groups. The dorso-lateral portion is composed of large, well-stained, multipolar cells scattered rather evenly through the medulla, while the cortex contains only a few scattered cells. This mass I have called the nucleus isthmi pars magno-cellularis (fig. 7). Medially and slightly ventrally, lies the remainder of the nucleus, closely applied to the pars magno-cellularis. It is composed of smaller, rounded, well-stained, closely packed cells, and is here called the pars parvo-cellularis (fig. 7). In addition to the division of the nucleus by the size of its cells, is the fact that the large-celled portion is also distinguishable by its dense neuropil background, a feature absent in the pars parvo-cellularis. The pars parvo-cellularis commences just caudal to the rostral pole of the pars magno-cellularis, and extends slightly caudal to the caudal pole of the latter (fig. 11). It is possible that the most caudal part of the pars parvo-cellularis may be related to the secondary gustatory nucleus, but I have not determined the exact connections of the latter nucleus, which is usually poorly developed in the reptilian brain.

The dorsal and lateral surfaces of the nucleus isthmi project on the external surface of the brain. Medially, it is related to the posterior corpus quadrigeminum, separated from it by the mesencephalic tract of the Vth nerve (fig. 21). The caudal pole of the nucleus comes into direct relationship with the lateral lemniscus (fig. 20). In all forms in which the nucleus isthmi has been described, this relationship with the lateral lemniscus has been mentioned, leading to the supposition that the nucleus isthmi is the homologue of the mammalian medial geniculate body. The caudal pole also comes to lie ventro-lateral to the cells of the nucleus cerebelli.

The hilus of the nucleus is on its rostro-lateral aspect. Fibres stream out

from here to the optic tectum (figs. 18, 19, 20). It could not be distinguished in my preparations whether these were tecto-isthmial or isthmio-tectal. Larsell (1924) described both types of fibres in the frog, recognisable in silver preparations. Huber and Crosby (1926) describe the tract as I have done, and although they could not distinguish the direction of the fibres, they drew an analogy from Larsell's description in the frog. Both tracts are probably present in *Sphenodon*.

The remaining connections of the nucleus isthmi can be briefly described. Fine non-medullated fibres run from the dorso-medial aspect of the nucleus to the anterior medullary velum, and mingle with the fibres of the commissura cerebelli, probably constituting a commissural tract with the nucleus of the opposite side. In the same direction, but more rostral, fine fibres pass to the posterior corpus quadrigeminum, intersecting on their way the mesencephalic tract of the Vth nerve. Larsell (1924), in the frog, describes a quadrigemino-isthmial tract, some of the fibres of which he suggests may possibly pass through the nucleus isthmi to join the isthmio-thalamic tract.

Larsell (1924) has described two further tracts in the frog, the tractus isthmio-thalamicus, and tractus commissura transversa. The tractus isthmio-thalamicus in the frog is composed of slender fibres, staining poorly, and I have been unable to find a corresponding tract in *Sphenodon*. Larsell's tractus commissura transversa is homologous to the commissure of Gudden, and Huber and Crosby (1926) have described the same tract under the heading of the decussatio supra-optica ventralis. Cairney (1926) has described this tract as the decussatio supra-optica ventralis in *Sphenodon*. It is clearly present in the optic chiasma, but the fibres, on being followed caudally through the mesencephalon, become intermingled with other tracts and cannot be traced further. I have been unable to prove their connection with the nucleus isthmi in *Sphenodon*.

Ventral to the nucleus isthmi is a nucleus of large multipolar, well-stained cells, flattened from side to side, and lying in the stream of the lateral lemniscus (figs. 7 and 8). This evidently corresponds to the nucleus lemnisci lateralis of Huber and Crosby (1929), and to the lateral part of the nucleus semilunaris of Kappers (1921).

FIBRE TRACTS

Tractus spino-cerebellaris ventralis

This is one of the largest fibre tracts terminating in the cerebellum. In the series examined, it can be traced some distance caudally in the medulla oblongata, but, unfortunately, most of the series do not extend as far caudally as the caudal limit of the IVth ventricle. The tract passes rostrally in the lateral wall of the medulla (fig. 27), and consists of well myelinated fibres. They ascend in this position as far rostrally as the roots of the Vth nerve, lying ventral to the dorso-spino-cerebellar fibres, and having the spino-tectal tract medially.

The tract then lies ventral to the Vth roots (fig. 26), and curves round the rostral limit of these roots to pass dorsally and medially to enter the cerebellar

commissure (fig. 20), where it can be distinguished as a distinct bundle. The majority of the fibres decussate in the rostral end of the cerebellar commissure where they lie just caudal to the decussation of the IVth nerve. The remainder of the fibres run dorsally to ramify in the granular layer of the cerebellum on the same side. In mid-sagittal section, the anterior medullary velum is practically negligible; the commissura cerebelli, here composed almost entirely of ventral spino-cerebellar fibres, lies adjacent to the caudal aspect of the decussatio veli, and a few of the most cephalic fibres of the commissure lie between the decussatio veli and the aqueduct of Sylvius.

The terminal ramifications of this tract appear to be in the granular layer.

Larsell (1926) discusses the varying degree of decussation of the ventral spino-cerebellar tracts in certain lizards and in a snake. The greatest amount of decussation in the specimens examined occurred in the snake, in which the cerebellar commissure appeared to be made up chiefly of decussating fibres of the ventral spino-cerebellar tract. This description for the snake is similar to that given by Huber and Crosby (1926) for *Alligator mississippiensis* and *Chrysemys marginata* where they name the tract the spino-cerebellar tract. It also corresponds to the condition seen in *Sphenodon*. The exact termination of these fibres in the cerebellum could not be accurately determined.

Huber and Crosby (1926) describe also a small cerebellar component accompanying the tractus spino-mesencephalicus in the alligator. They are undecided whether this tract corresponds to Gower's ventral spino-cerebellar tract of mammals, or whether the spino-cerebellar tract of the alligator carries fibres which, in higher forms, are incorporated into Gower's tract.

Analogous to the spino-tectal tract of other reptiles, the spino-tectal tract in *Sphenodon* is found ventral and medial to the ventral spino-cerebellar tract and lateral to the lateral lemniscus (fig. 24). The tract leaves the ventral spino-cerebellar tract at the level of the roots of the Vth nerve, and passes rostrally into the mid-brain. During its course through the medulla, this tract is with difficulty distinguishable from the lateral lemniscus. I have been unable to find the cerebellar component of this spino-tectal tract described by Huber and Crosby.

Tractus spino-cerebellaris dorsalis

Larsell (1926) describes a tractus spino-cerebellaris dorsalis (or bulbo-cerebellaris) in the reptiles. As represented in *Anniella*, the tract passes lateral to the vestibular nucleus, and may be traced caudally as a distinct bundle through the greater part of the bulb, losing its identity in the caudal region of the medulla oblongata. Larsell favours the view that it is a spinal rather than a bulbar tract. The above description applies almost exactly to the tract in *Sphenodon*. Its caudal origin could not be exactly determined. It passes rostrally along the lateral surface of the bulb becoming all the time more dorsal (fig. 27). It passes through the roots of the Vth nerve (figs. 20, 26) and runs into the cerebellum in conjunction with the vestibulo-cerebellar tract.

Huber and Crosby (1926) do not mention a dorsal spino-cerebellar tract. Though they suggest that the cerebellar component of the spino-mesencephalic tract is the homologue of the ventral spino-cerebellar tract of mammalian forms, they do not therefore attempt to homologise the spino-cerebellar tract to the alligator (ventral spino-cerebellar tract of *Sphenodon*) with the mammalian dorsal spino-cerebellar tract. The general view is to consider this reptilian ventral spino-cerebellar tract as the homologue of part of Gower's complex, and the reptilian dorsal spino-cerebellar tract as the homologue of the mammalian tract of the same name.

Tractus vestibulo-cerebellaris

This tract in *Sphenodon* is similar to that described in other reptiles. The majority of its fibres take origin in the superior vestibular nucleus. From there some fibres curve around the lateral recess (fig. 25) to pass into the stratum granulare, some to terminate on the same side and others to cross to the opposite side. Other fibres, mainly from the lateral vestibular nucleus, pass rostrally into the auricular lobe. I have been unable to find a direct vestibulo-cerebellar tract.

In the series examined, no definite tractus trigemino-cerebellaris was seen. Fibres passing rostrally from the trigeminal nucleus became so intermingled with other fibre tracts that I was unable to establish definitely a connection between this nucleus and the cerebellum. This connection was established in the frog by Larsell (1923), but he was unable to make a definite statement concerning it in the snakes and lizards (Larsell, 1926).

Tractus cerebello-tegmentalis

In addition to the brachium conjunctivum, there are efferent fibres from the ventral cerebellar eminence, possibly also from other parts of the cerebellum, passing caudally and ventrally into the tegmentum of the medulla oblongata. These fibres are few and scattered and are mainly non-medullated.

At their commencement, they are closely associated with the fibres of the brachium conjunctivum, but lie slightly more laterally. Huber and Crosby (1926), in the alligator, have suggested that this tract may be a differentiated portion of the tractus cerebello-tegmentalis mesencephali.

On being traced caudally, these fibres extend close to the motor nucleus of the Vth nerve, dorsal to which they pass. They then decussate in the midline ventral to the fasciculus longitudinalis medialis. The fibres thereafter spread out and become lost in the grey matter of the medulla.

This tract therefore places the motor nucleus of the Vth nerve, and undoubtedly other bulbar nuclei, under the influence of the cerebellum. It is evidently the same tract as that figured by Kappers (1921), for *Crocodilus porosus*, as the tractus cerebello-motorius.

Brachium conjunctivum

This tract has already been noted in connection with the nucleus cerebelli. Its fibres have their origin partly in this nucleus and partly in some more dorsal structure in the cerebellum. Larsell (1923) suggests that, in the frog, fibres of this tract originated in part as axons of Purkinje cells. This could not be accurately ascertained in *Sphenodon* preparations.

The tract is best seen in sagittal sections stained by the Cajal method (figs. 19, 20). The fibres are fine and mainly non-medullated. They are collected in a definite bundle only at their commencement. Beyond that they become more scattered, and pass rostrally and ventrally into the mid-brain. They decussate ventral to the fasciculus longitudinalis medialis, but their final termination could not be determined.

Tractus tecto-cerebellaris

This tract has been described in reptiles by Huber and Crosby (1926) for *Chrysemys marginata*, and by Larsell (1926) for *Sceloporus* and *Gerrhonotus*. A similar tract can be seen in *Sphenodon* in Cajal series, but could not be distinguished in Weigert preparations. In the silver preparations, very fine fibres can be seen running from the tectal regions first ventrally, and then caudally, dorsal to the corpus quadrigeminum posterior. Throughout their course they remain close to the midline, passing, however, dorsal to the mesencephalic tract of the Vth nerve and then ventral to the decussating fibres of the IVth nerve. They enter the anterior border of the cerebellar commissure, beyond which point they could not be traced.

Owing to its intimate relationship with certain cerebellar structures, the IVth nerve may be aptly included in the description at this stage.

Nervus trochlearis

The nucleus of the IVth nerve lies in the floor of the posterior part of the aqueduct of Sylvius dorsal to the medial longitudinal fasciculus (figs. 1, 7). The fibres emerge from the nucleus on its dorso-lateral surface, curving just dorsally and laterally and then dorsally and medially round the aqueduct (figs. 21, 22). The root is composed of a compact bundle of large coarsely medullated fibres which form, in some sections, a definite projection into the aqueduct (fig. 22). The decussation of fibres occurs in two stages, close to the dorsal surface of the isthmial region. About half the fibres decussate and emerge from the brain in the midline, and the remainder pass across to the opposite side, dorsal to the aqueduct, to emerge from the brain surface just medial to the nucleus isthmi. The two bundles immediately unite, forming the IVth nerve, which passes rostrally and ventrally over the dorsal surface of the nucleus isthmi (fig. 3).

The decussation of the IVth nerve is a very definite structure in *Sphenodon* and lies immediately rostral to the cerebellum (fig. 1). The most caudal portion

of the decussation in the midline may even lie dorsal to the cerebellar commissure which here is mainly composed of fibres from the ventral spino-cerebellar tract.

Larsell (1924) describes a third root in the frog which enters the cerebellum proper, joining the cerebellar commissure. He suggests that some fibres are uncrossed, and join the mesencephalic tract of the Vth nerve to pass to the region of the motor nucleus of the Vth nerve. McKibben (1913) states that, in *Necturus*, there appear to be a few uncrossed fibres which enter the IVth nerve, and which seem to be larger fibres than those which make up the trochlear nerve. They belong to the mesencephalic root of the trigeminal nerve which lies here beneath the trochlear nerve (fig. 22).

Larsell (1923) suggests that this caudal root in *Rana pipiens* contains muscle sense fibres, whose distribution is evidently to the trochlear muscle.

I have been unable to find anything corresponding to Larsell's third root entering the cerebellum of *Sphenodon*. The relationship between the IVth nerve and the mesencephalic tract of the Vth nerve is discussed in the description of the latter tract.

Tractus mesencephalicus trigemini

The fibres of the mesencephalic tract of the Vth nerve are easily discernible as they leave the optic tectum and, passing dorsally over the posterior corpora quadrigemina (fig. 21), descend on their posterior surface to reach the most ventral level of these bodies. The tract consists of fibres, heavily myelinated, arranged in small bundles, and conspicuous in Weigert series. The tract is seen as a ribbon which appears vertical in cross section. The fibres then pass caudally and also laterally to a somewhat more ventral plane. They thus reach the decussation of the IVth nerve where they turn still more laterally and ventrally to pass between the nucleus isthmi laterally and the IVth nerve medially (fig. 22). It is in this region in *Sphenodon* that some of the most medial fibres of the tract appear to pass into the decussation of the IVth nerve.

McKibben (1913) in *Necturus*, and Davidson Black (1917), and Larsell (1923), with regard to the relations in the frog, speak in favour of dendrites of the mesencephalic root of the Vth nerve joining the root fibres of the IIIrd and IVth nerves to leave the brain with their roots. This statement, Larsell says, cannot be proved with certainty in normal preparations. In the series examined by me, I have been unable to trace definitely a fibre from the mesencephalic tract of the Vth nerve into the root of the IVth nerve, though it is impossible to state that such a relationship does not exist.

Herrick (1914) describes for *Necturus*, fibres of the mesencephalic tract of the Vth nerve passing through the cerebellar commissure to reach the more posterior cells of the nucleus magno-cellularis tecti of the opposite side. In *Sphenodon*, this latter condition may occur, as a few fibres can be traced from the tract under discussion into the cerebellar commissure in its anterior part. The termination of these fibres is probably as Herrick has described for *Necturus*.

From this region the mesencephalic tract of the Vth nerve passes laterally and caudally, becoming here more ventral to the cerebellum. It lies between the brachium conjunctivum ventro-medially and the vestibulo-cerebellar tract dorsally and laterally. The tract then runs caudally, ventro-medial to the vestibulo-cerebellar tract (figs. 23, 24), and is seen in cross section as a bundle flattened from side to side. It continues in this course to reach the nuclei of the Vth nerve.

Decussatio veli

This structure in *Sphenodon* is closely related to the commissura cerebelli (fig. 1). It lies immediately rostral to the cerebellum and is composed of the decussating fibres of the trochlear nerve, the fine fibres of the tractus tecto-cerebellaris, and possibly some fibres from the mesencephalic tract of the Vth nerve.

Commissura cerebelli

The cerebellar commissure is rather a massive structure and contains several groups of fibres. Its main constituents are the decussating fibres of the ventral spino-cerebellar tract (fig. 23). Included in it also, are fibres from the mesencephalic tract of the Vth nerve, and a large number of fibres connecting the two halves of the cerebellum.

SUMMARY

The cerebellum of *Sphenodon* is a very simple structure and presents no outstanding differences from the cerebella of other lizards. It appears to be a primitive type from which have sprung the specialised forms as seen in *Sceloporus* and *Gerrhonotus*.

It is of great interest to note the close similarity of the external features of the cerebellum of *Sphenodon* to those of the cerebellum of the 27 mm. human foetus, when also the developing telencephalon of *Sphenodon* at one stage has been shown to resemble that of the 11·8 mm. human embryo.

Its internal structure clearly shows the three typical layers, molecular, Purkinje, and granular. A definite nucleus cerebelli is present, closely related to the superior vestibular nucleus both by its proximity and by fibre tracts. The nuclear mass has not yet divided into two as described in other types of lizards.

The cerebellum of *Sphenodon* possesses practically all the main fibre tracts which are described for other lizards. These include two spino-cerebellar tracts, dorsal and ventral, vestibulo-cerebellar and tecto-cerebellar, as well as the brachium conjunctivum and cerebello-tegmental fibres.

The nucleus isthmi is well developed and can be divided into two distinct nuclear masses, each with its own connections. It bears its usual relation to the lateral lemniscus and the optic tectum as a cell station between the *Nucleus cochlearis* and the optic tectum.

EXPLANATION OF FIGURES

Figs. 1 to 14 represent sections stained by the toluidin blue method, and figs. 15 to 27 sections stained by the Weigert method.

Figs. 6 to 27 have been drawn to the same degree of magnification by projection of the actual sections. Figs. 1 to 5 are drawn to a magnification $\frac{2}{3}$ of the above.

The cell size is not strictly to scale, but, where possible, variations in the size of the cells is indicated.

ABBREVIATIONS USED IN FIGURES

aur.l.	Auricular lobe.
aq.S.	Aqueduct of Sylvius.
br.conj.	Brachium conjunctivum.
cb.	Cerebellum.
co.cb.	Commissura cerebelli.
c.p.q.	Corpus quadrigeminum posterior.
dec.vel.	Decussatio veli.
f.r.	Formatio reticularis.
l.l.	Lateral lemniscus.
med.obl.	Medulla oblongata.
m.l.f.	Median longitudinal fasciculus.
n.III	Third nerve.
n.IV	Trochlear nerve.
n.V	Trigeminal nerve.
nuc.cb.	Nucleus cerebelli.
nuc.isth.	Nucleus isthmi.
nuc.isth.p.m.	Nucleus isthmi pars magno-cellularis.
nuc.isth.p.p.	Nucleus isthmi pars parvo-cellularis.
nuc.vest.	Nucleus vestibularis.
nuc.vest.sup.	Nucleus vestibularis superior.
nuc.III	Nucleus of the third nerve.
nuc.IV	Nucleus of the fourth nerve.
nuc.Va.	Afferent nucleus of the trigeminal nerve.
nuc.Ve.	Efferent nucleus of the trigeminal nerve.
op.tect.	Optic tectum.
r.III	Root of the third nerve.
r.IV	Root of the fourth nerve.
r.V	Root of the fifth nerve.
r.Va.	Afferent root of the fifth nerve.
r.Ve.	Efferent root of the fifth nerve.
r.VIId.	Afferent root of the seventh nerve.
r.VIIe.	Efferent root of the seventh nerve.
st.gr.	Stratum granulare.
st.mol.	Stratum moleculare.
st.Pur.	Stratum Purkinje.
sul.post.	Sulcus posterior.
tr.isth.tect.	Isthmio-tectal tract.
tr.mes.V	Mesencephalic tract of the fifth nerve.
tr.sp.cb.d.	Dorsal spino-cerebellar tract.
tr.sp.cb.v.	Ventral spino-cerebellar tract.
tr.sp.tect.	Spino-tectal tract.
tr.vest.cb.	Vestibulo-cerebellar tract.
vent.III	Third ventricle.
vent.IV	Fourth ventricle.
VIII.coch.	Cochlear nucleus.
VIII.vest.	Vestibular nucleus.

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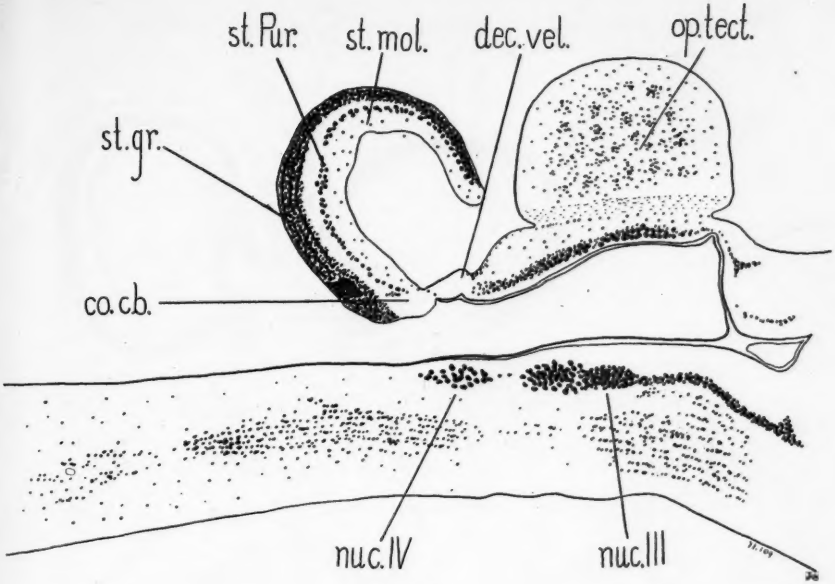


Fig. 1

Figs. 1–5. Sagittal sections of one brain from medial to lateral.

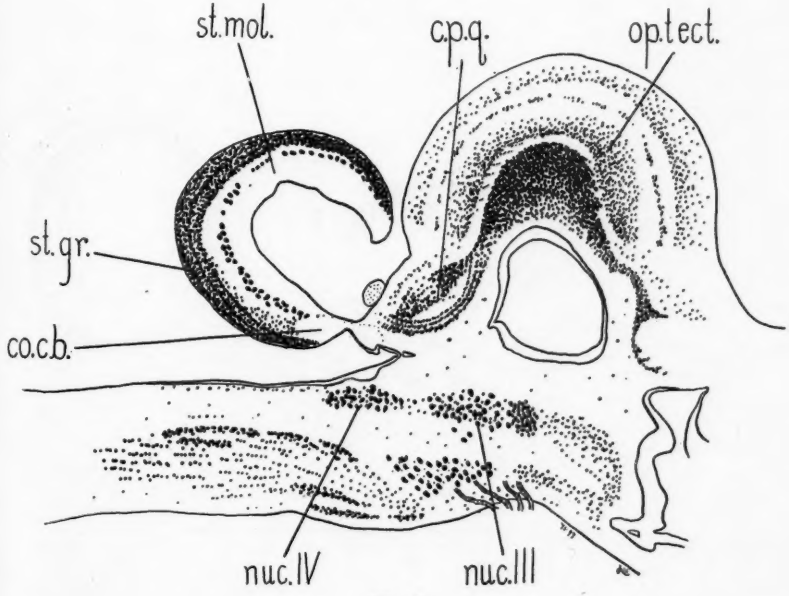
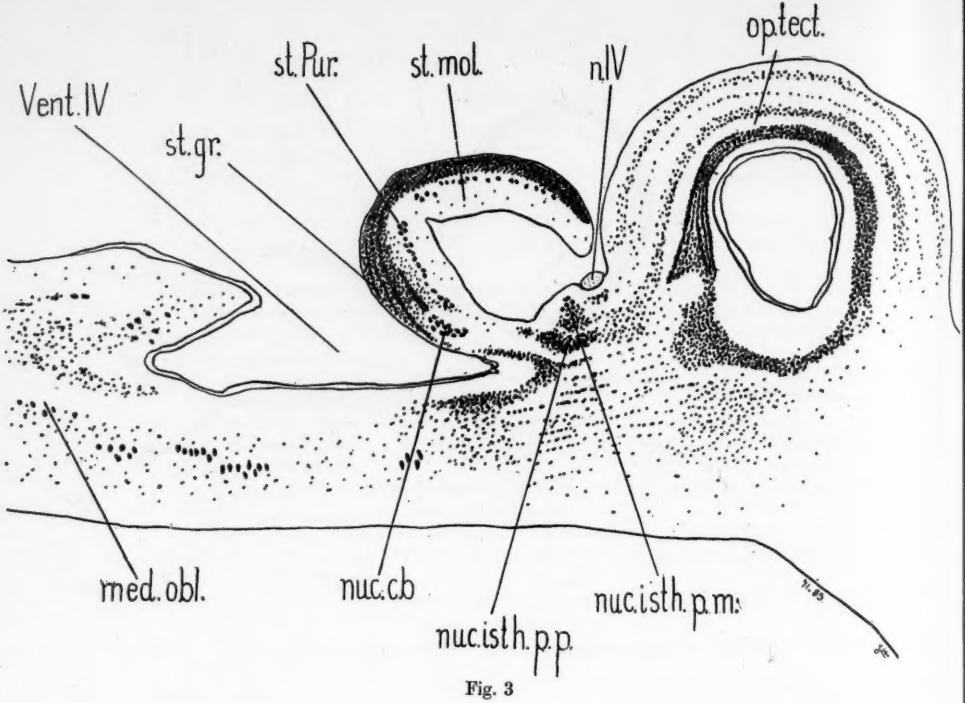


Fig. 2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nuc.isth.p.m.

Fig. 3

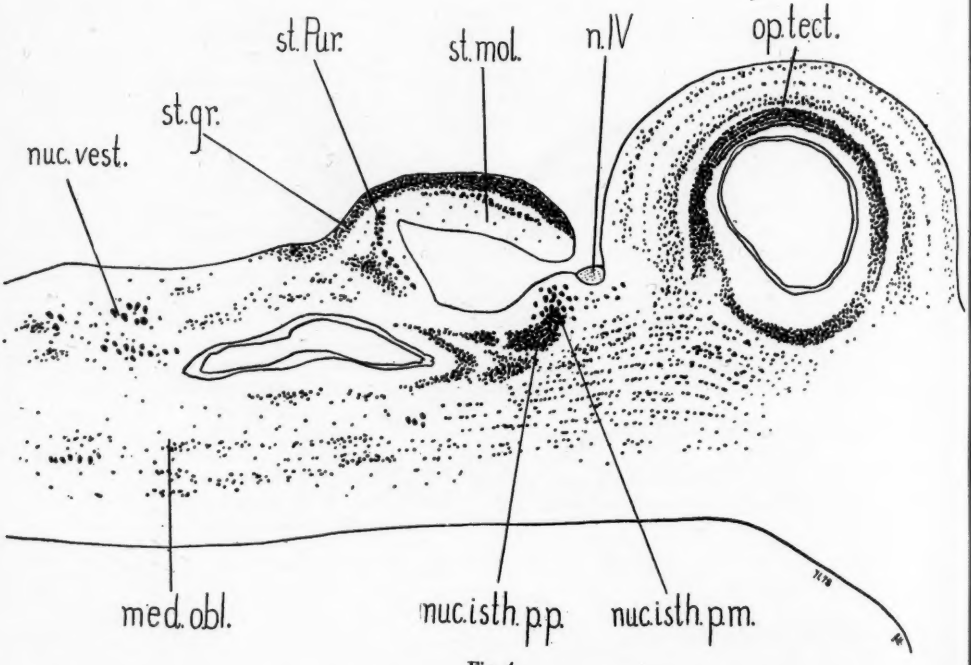
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Fig. 4

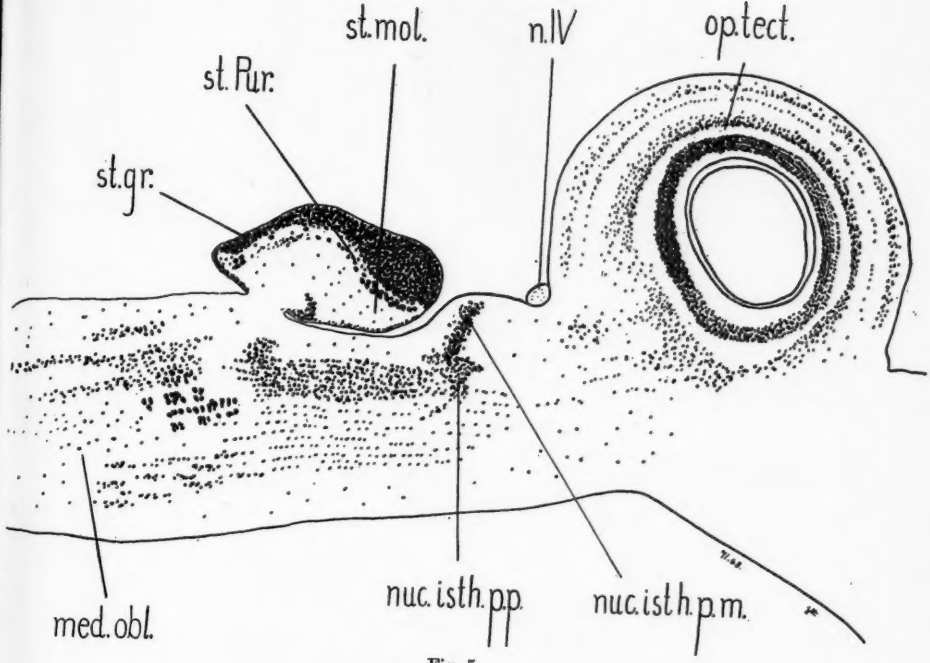


Fig. 5

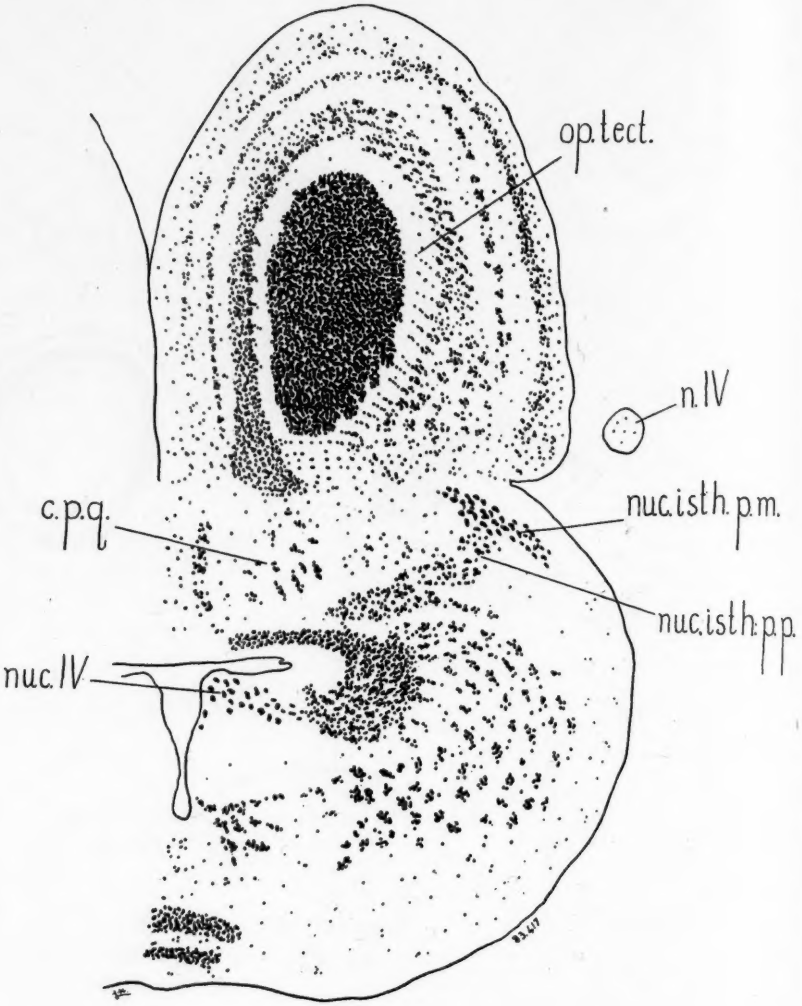
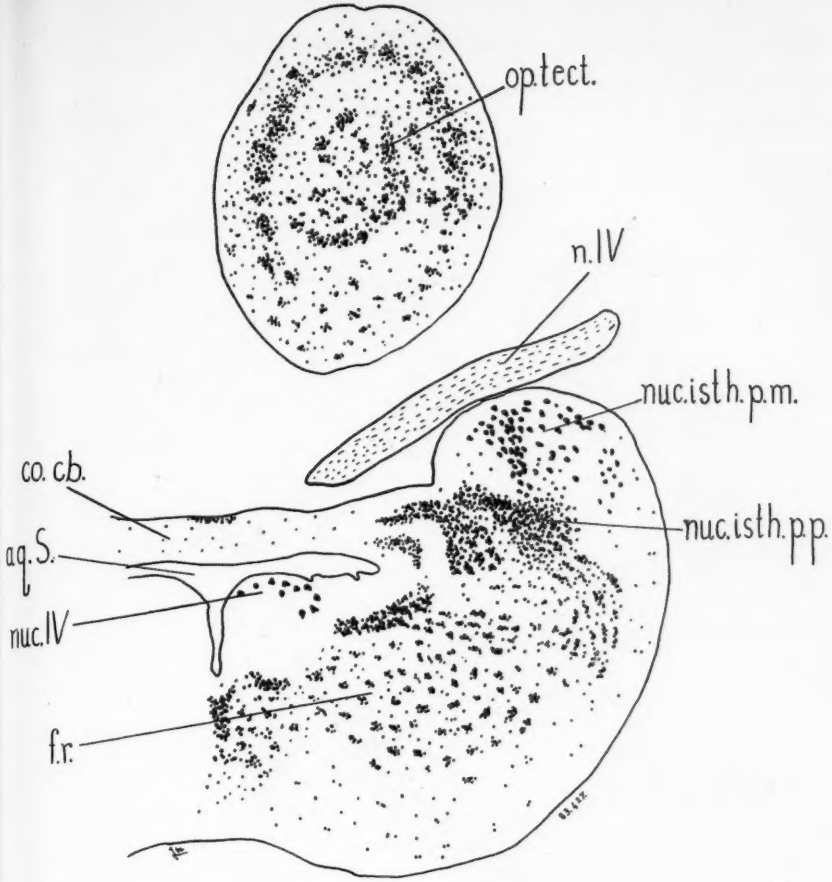


Fig. 6

Figs. 6–10. Transverse sections from before back through the cerebellar regions.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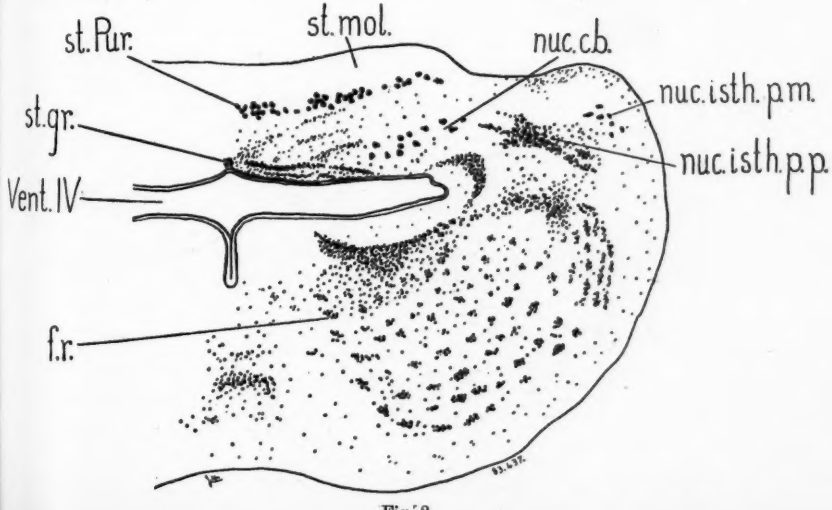
aq. S.
nuc.IV
f.r.

Fig. 7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Vent.IV
f.r.

Fig. 8

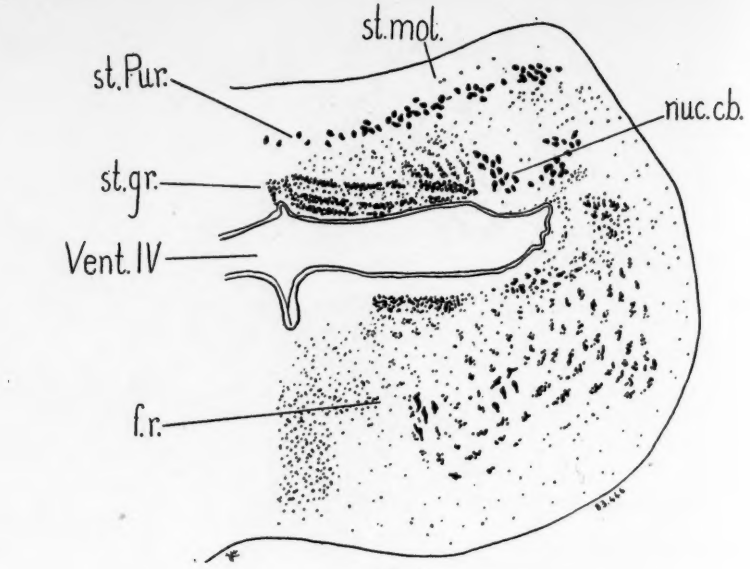
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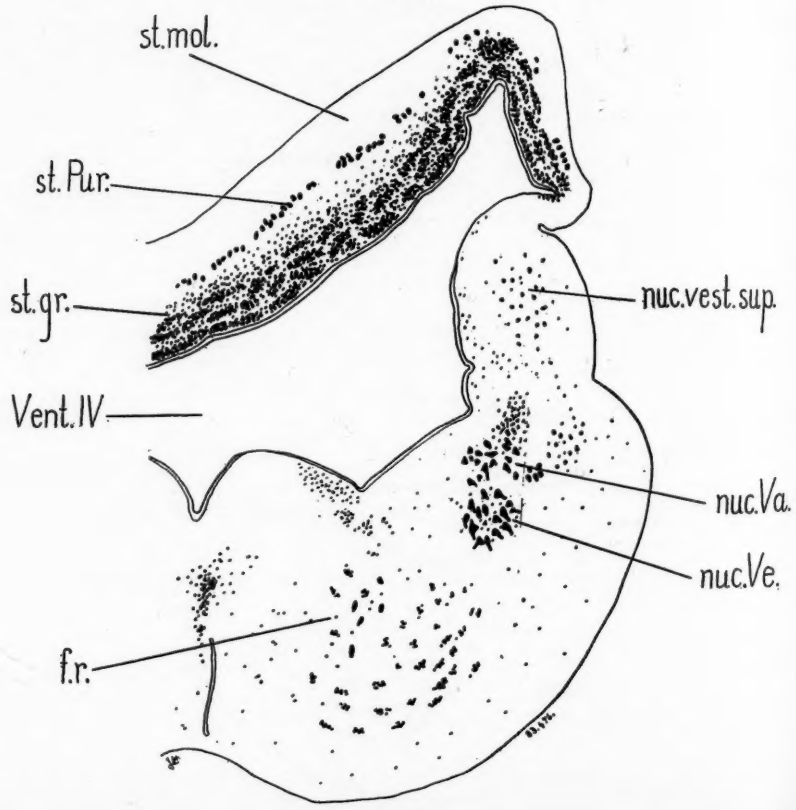
Fig. 9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Vent.IV
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nuc.Ve.
f.r.

Fig. 10

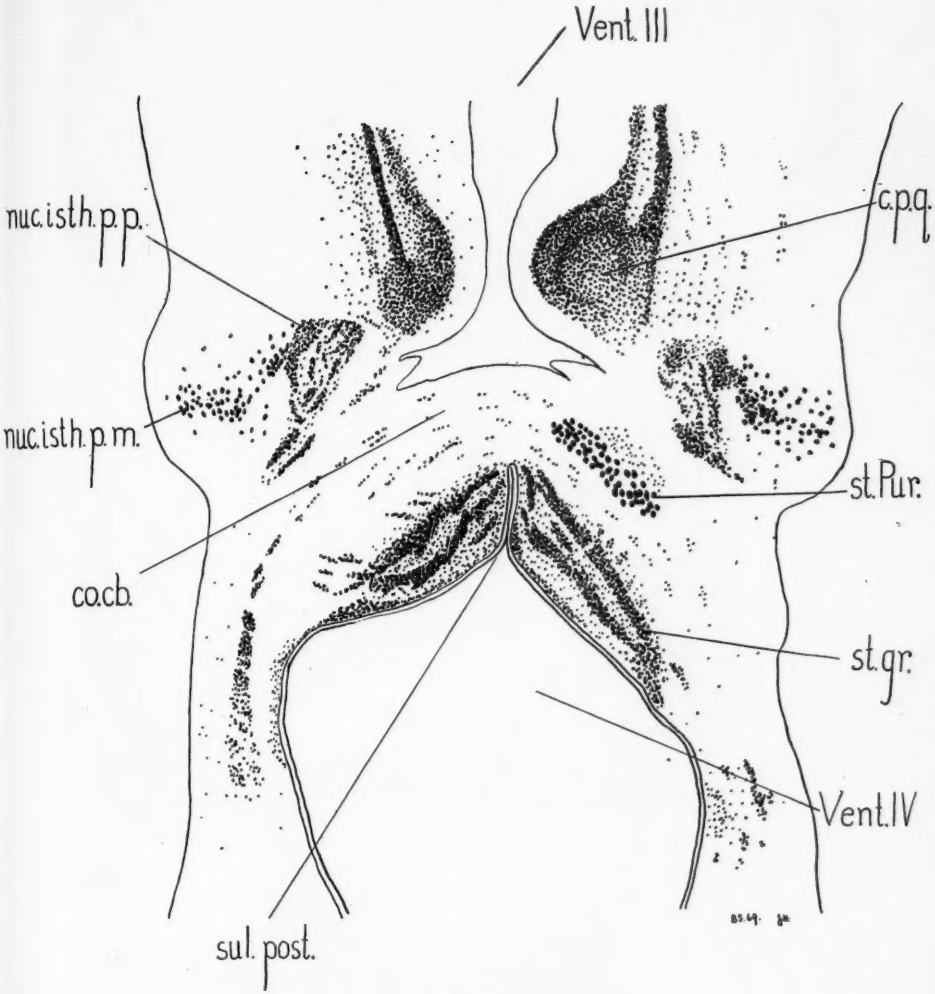


Fig. 11

Figs. 11–13. Horizontal sections of one brain from ventral to dorsal. Fig. 13 shows three separate sections through the cerebellum itself from ventral to dorsal.

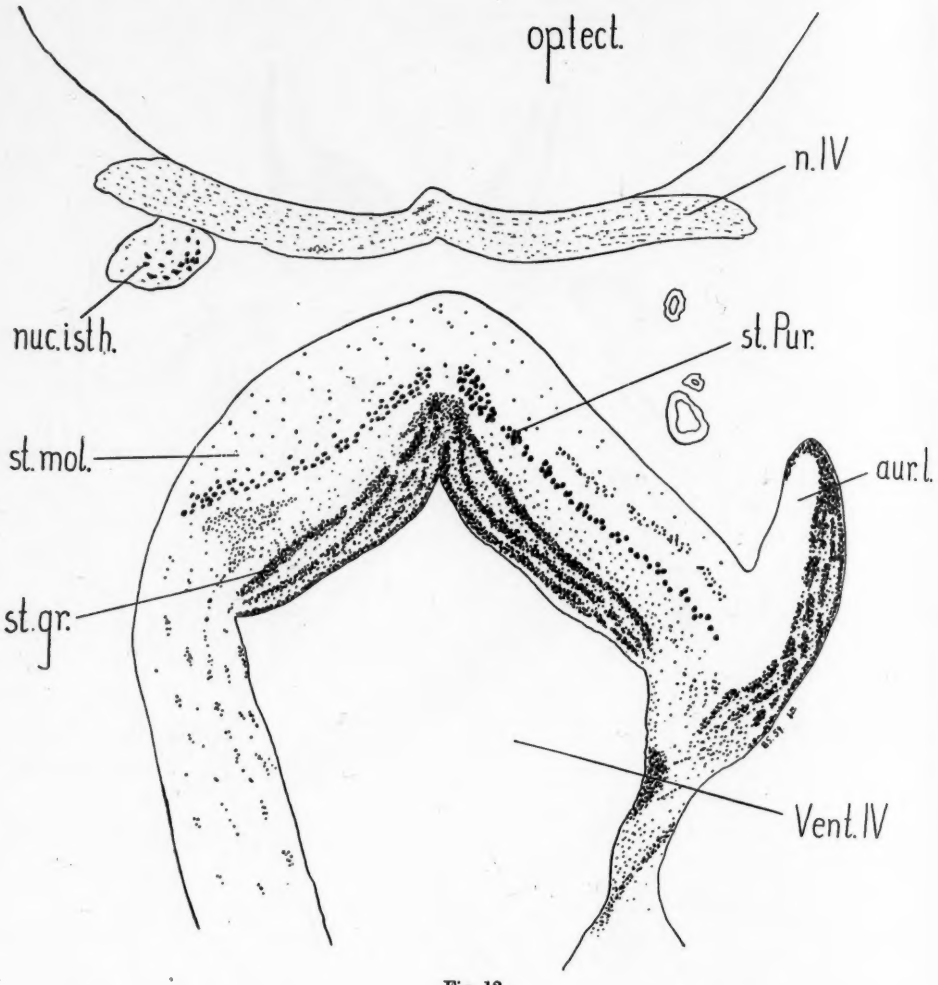


Fig. 12

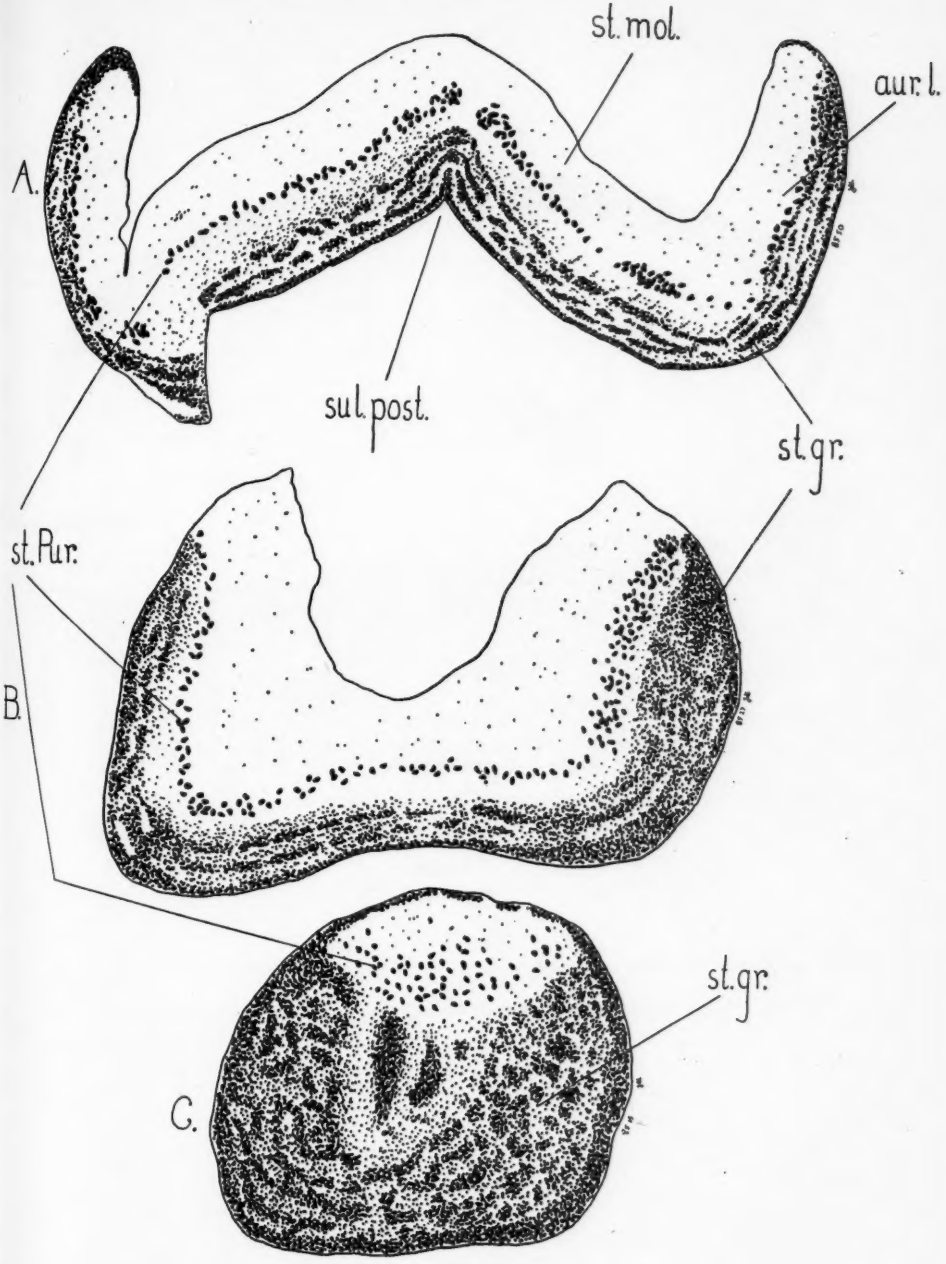


Fig. 13

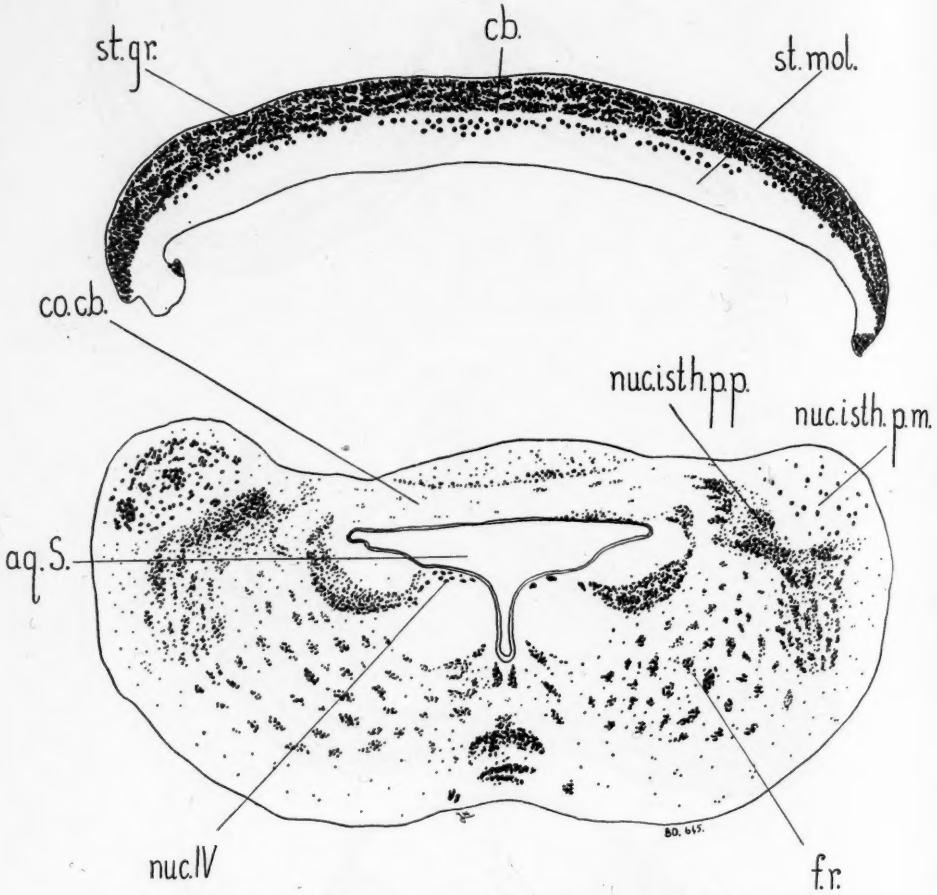


Fig. 14. This is a typical transverse section through the cerebellar region of *Sphenodon*.

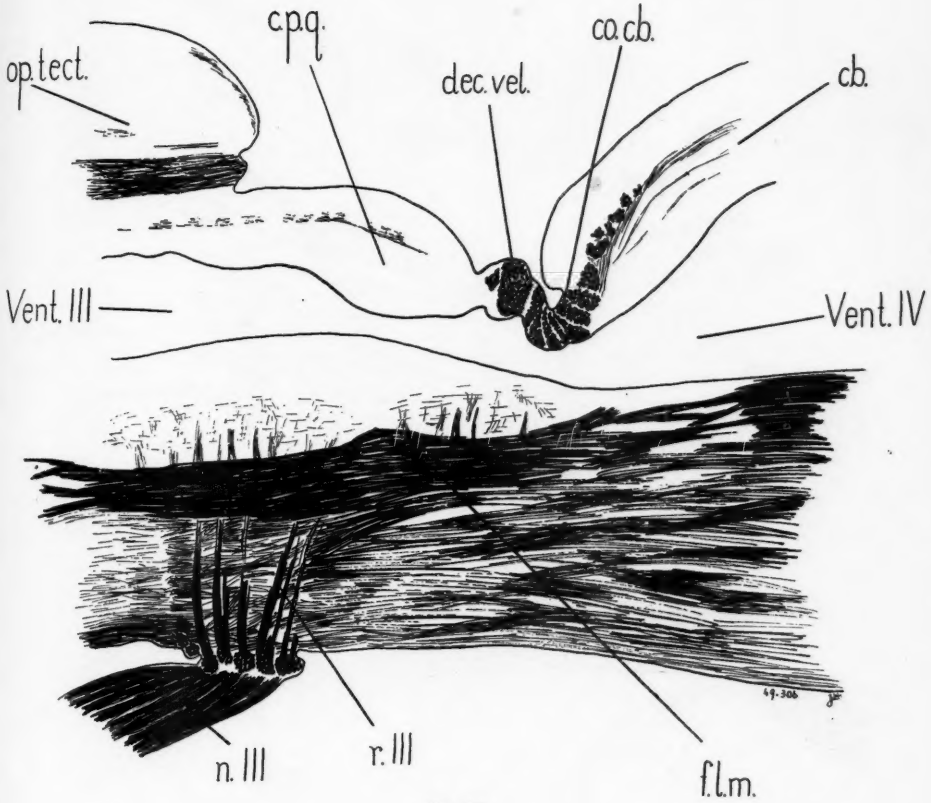


Fig. 15

Figs. 15–20. Longitudinal sections of one brain from medial to lateral.

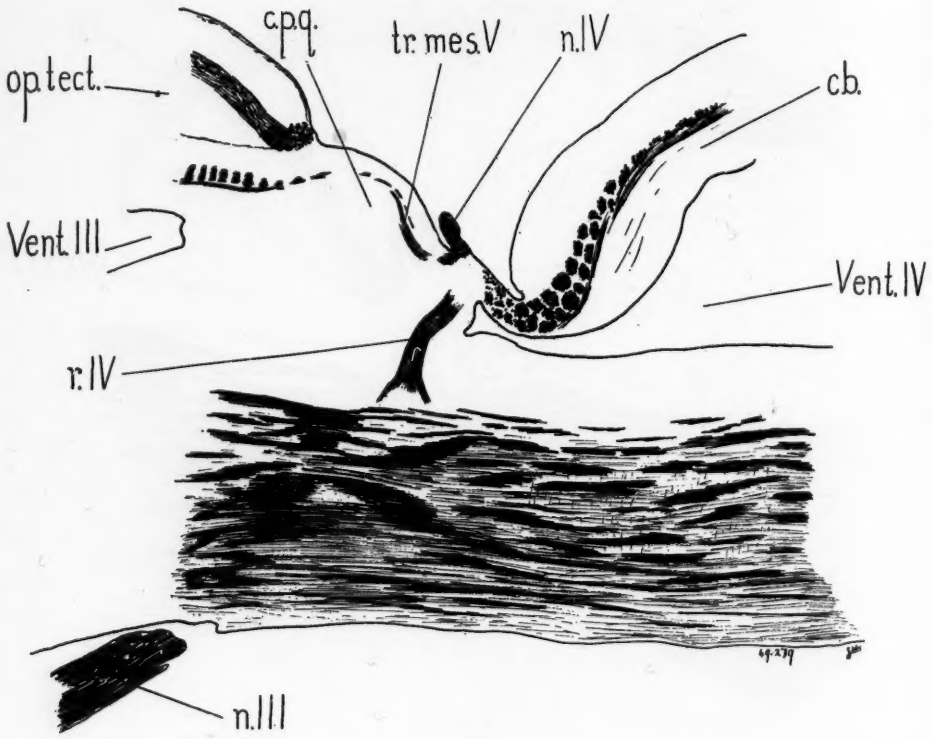
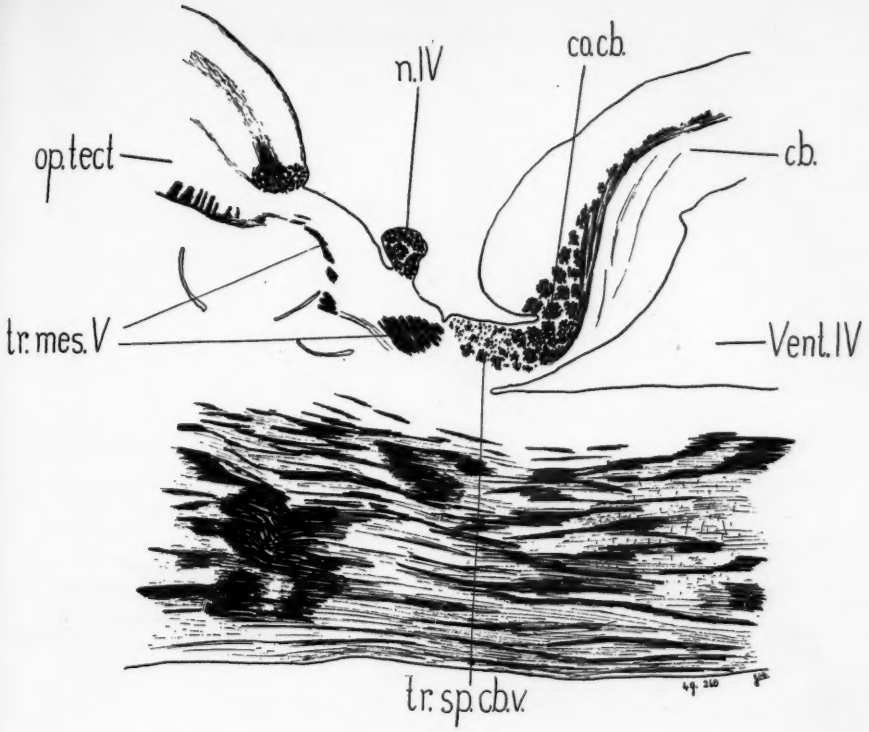


Fig. 16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Vent.IV
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Fig. 17

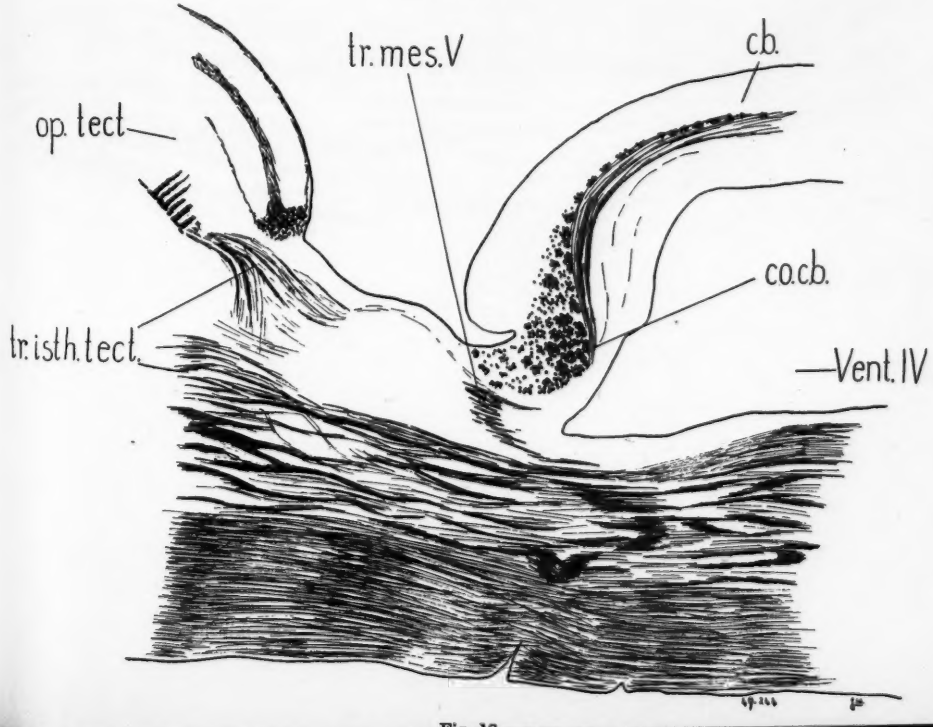
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Fig. 18

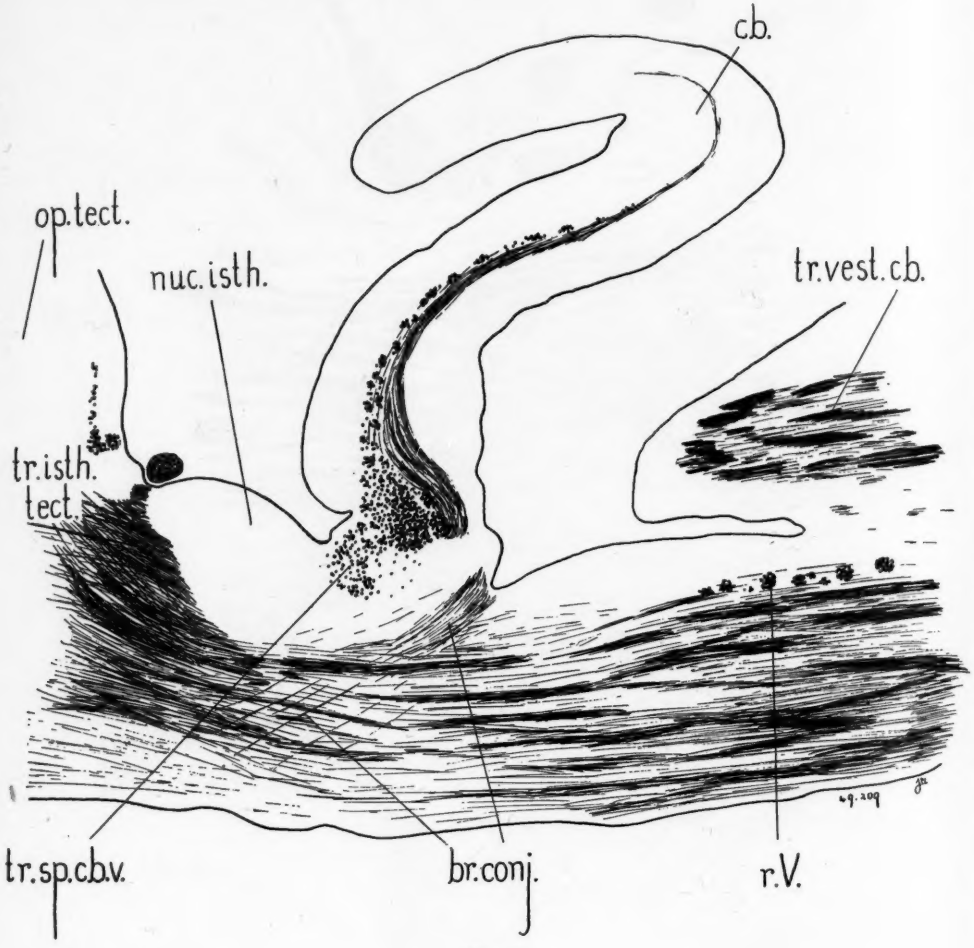
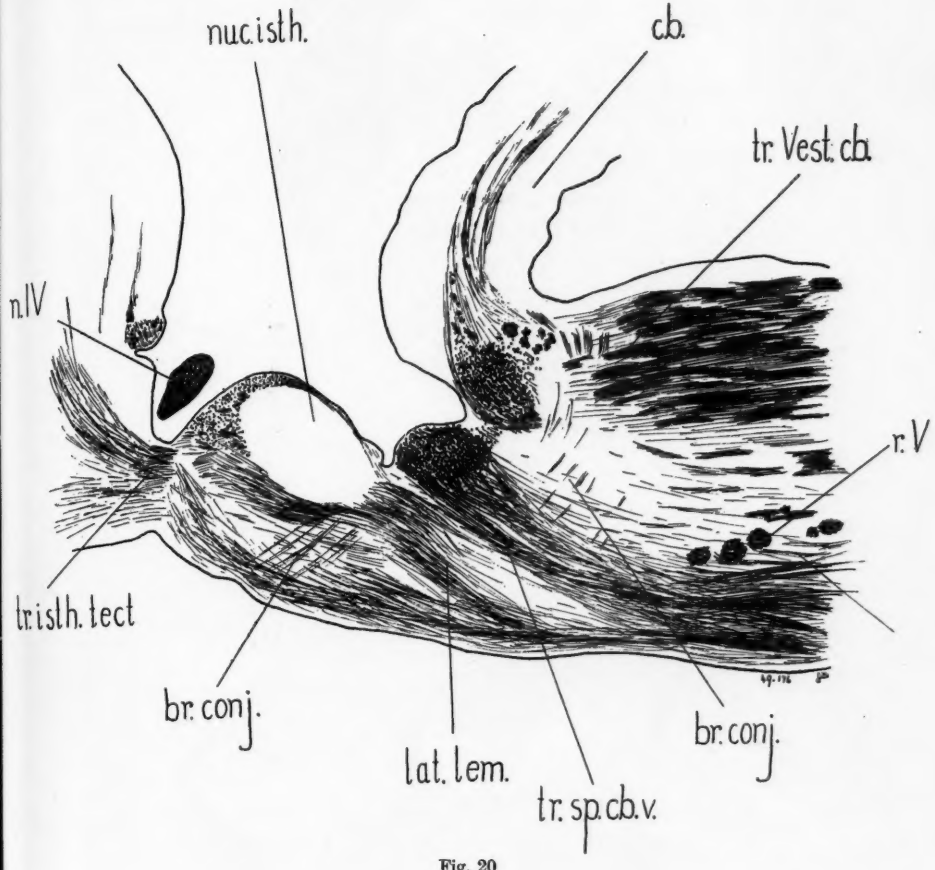


Fig. 19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cb.
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br. conj.
lat. lem.
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br. conj.

Fig. 20

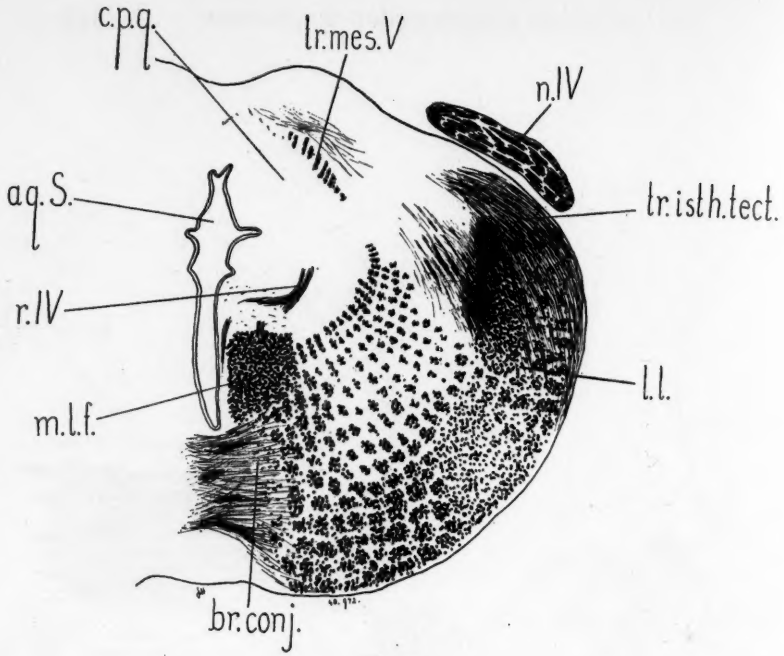

Fig. 21

Figs. 21–27. Transverse sections from before back through the cerebellar region of one brain.

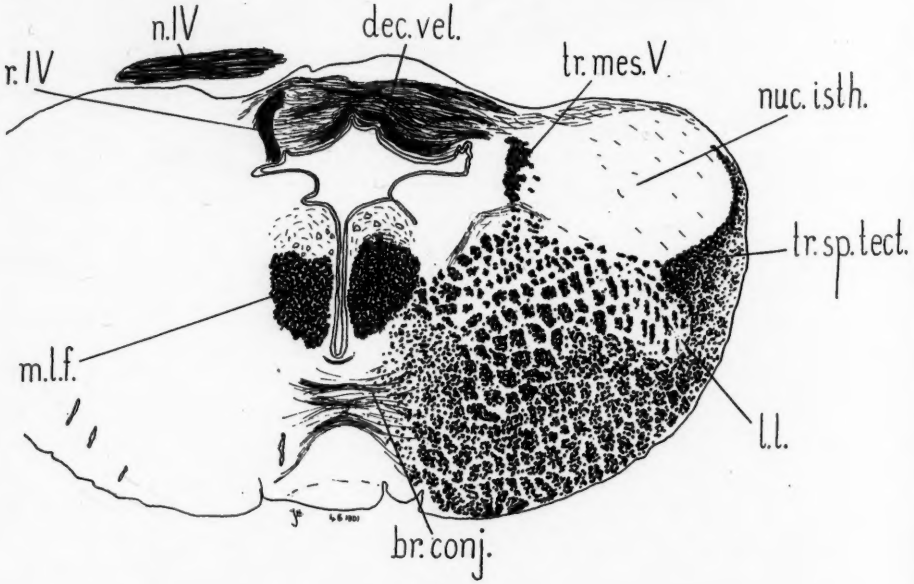

Fig. 22

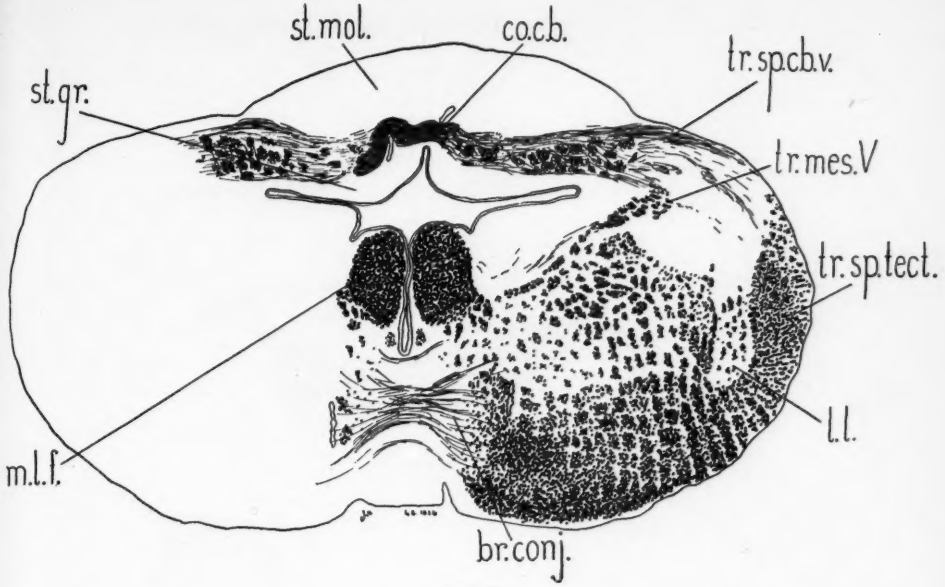
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Fig. 23

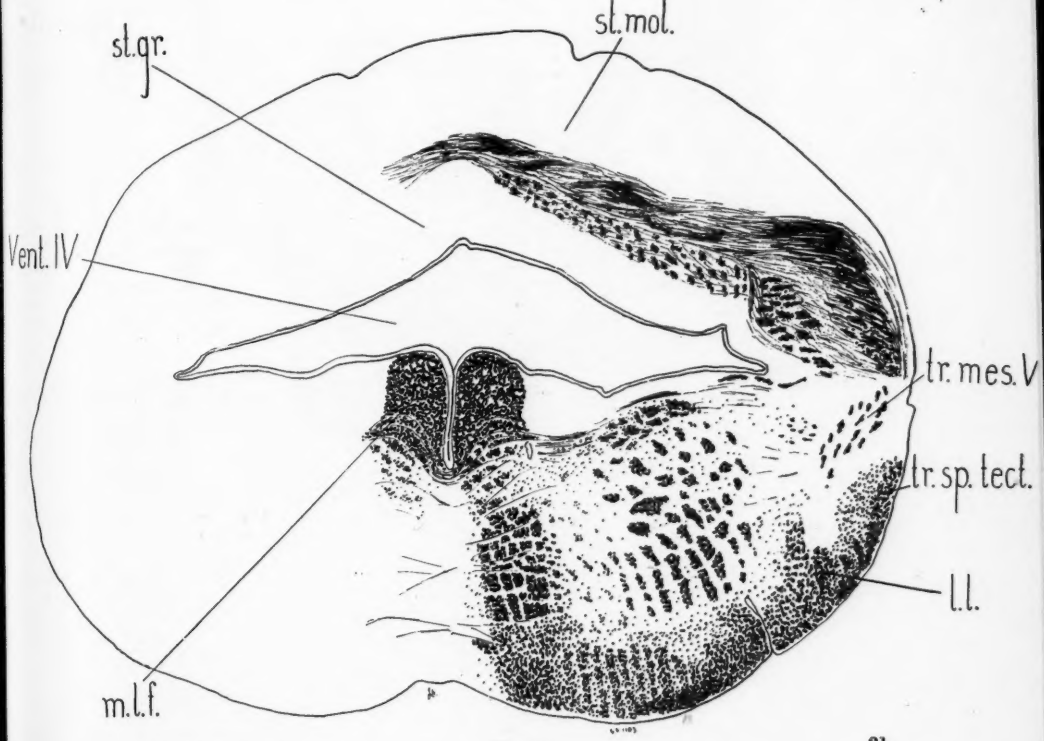
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Fig. 24

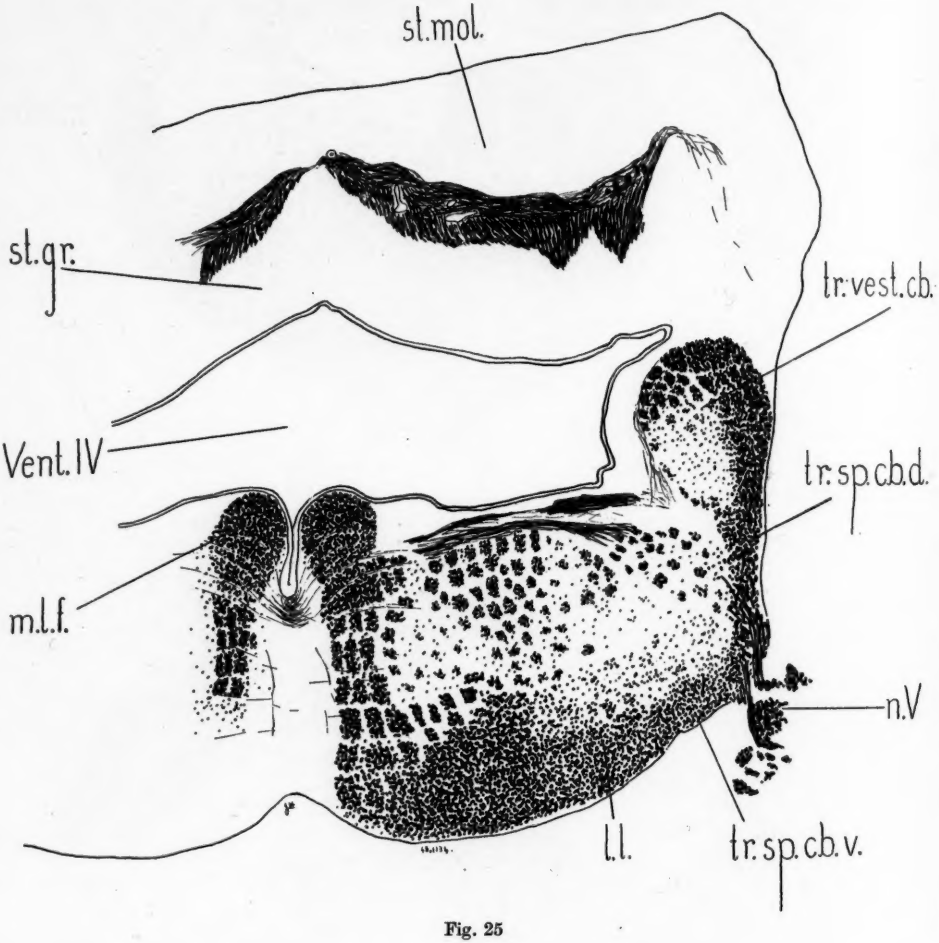
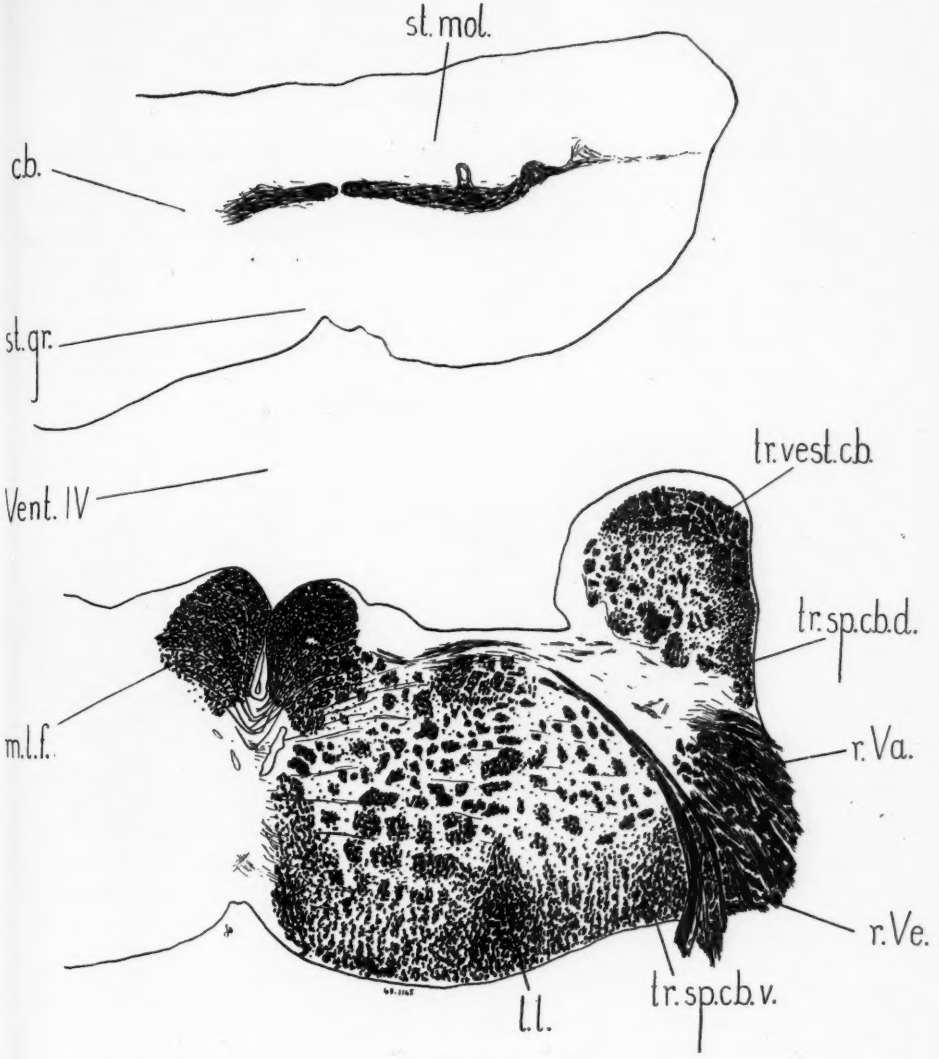


Fig. 25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cb.
st. gr.
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r. Va.
r. Ve.
l. l.
tr. sp. cb. v.

Fig. 26

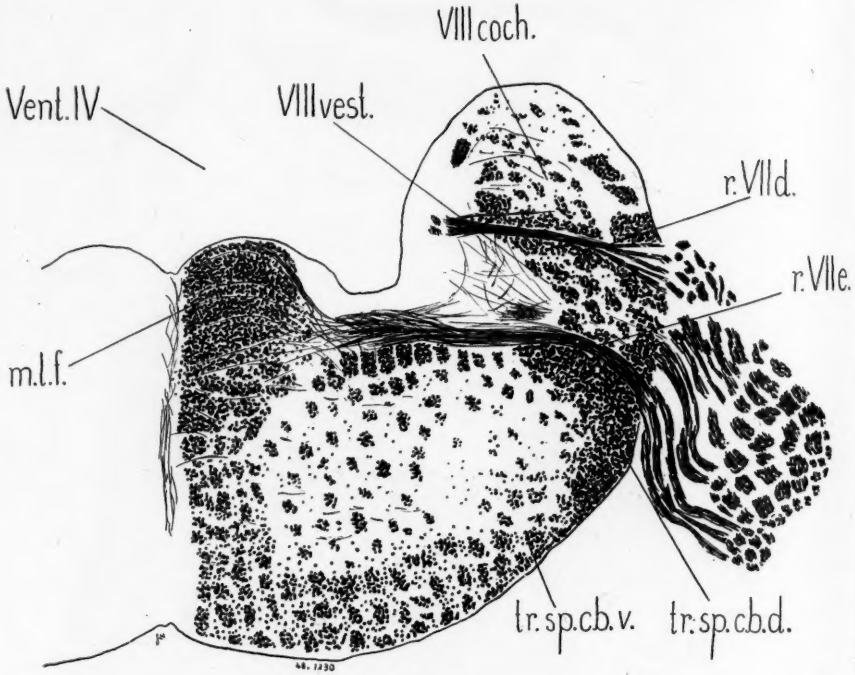

Fig. 27

THE INTRA-MANDIBULAR COURSE OF THE INFERIOR DENTAL NERVE

By C. STARKIE, B.Sc. and D. STEWART, M.Sc., M.R.C.S., L.R.C.P.

Until two years ago it was generally accepted by dental surgeons that the inferior dental nerve of one side overlapped as far, at least, as the canine tooth of the opposite side. This statement was based on the results which were obtained from block anaesthesia of that nerve. Stewart and Wilson (2), while carrying out an investigation into the results of regional anaesthesia, obtained evidence which suggested that this overlap frequently did not occur, and that when it did it never extended further, at the most, than the lateral incisor. On account of the discrepancies between these views, it was felt that a re-investigation of the intra-osseous course of the inferior dental nerve might give definite information as to its precise termination. It was with this aim therefore that the present investigation was undertaken.

The material used was taken from dissecting room subjects, supplemented by the mandibles of some of the commoner mammals. The bones were decalcified in 10 per cent. nitric acid and then dissected with mounted needles under a dissecting microscope. This was found to be somewhat difficult on account of the small size of many of the nerves, which often resembled strands of fibrous tissue, and also because of the fat associated with the nerves. The latter was removed by means of ether, and the nervous nature of the fibres was determined by establishing their continuity with the main nerve trunk. In doubtful cases a small portion of the structure was removed and examined microscopically.

The inferior dental nerve is usually described as entering the mandibular foramen in the form of a single trunk which lies anterior and superior to the inferior dental artery. It then gives off dental branches which may form a plexus from which the actual fibres to the teeth arise. The main trunk ends by dividing into the mental and incisive branches.

In 1927 (1) Olivier gave a much fuller account, and described two types in the arrangement of the main trunk of the inferior dental nerve. In Type I, seen in 66 per cent. of his dissections, the nerve formed a single bundle until it divided into its terminal branches at the mental foramen. The filaments to the teeth came off from the undivided trunk a little posteriorly to the roots that they were going to supply.

In Type II, seen in 34 per cent. of his dissections, the nerve divided into a larger mental branch which passed out at the mental foramen, and a smaller dental branch which formed a plexus and supplied the teeth. The incisor nerve did not form a separate branch, but was an extension of the dentinal plexus.

Olivier found that the incisor nerves lay free in the spongy bone and had neither a fibrous nor a bony sheath. These nerves took one of three directions:

(*a*) They passed forwards and upwards, by a direct route, to the alveus of the central incisors.

(*b*) The first ran horizontally, then turned sharply upwards into the alveus of the central incisors.

(*c*) They passed forwards and downwards towards the lower border of the jaw, where a branch was sometimes given off to the bone, and then turned upwards towards the central incisors.

No communicating branches between the right and left nerves were seen.

In our dissections certain observations were made which differ in some respects from those of Olivier, and these will now be described.

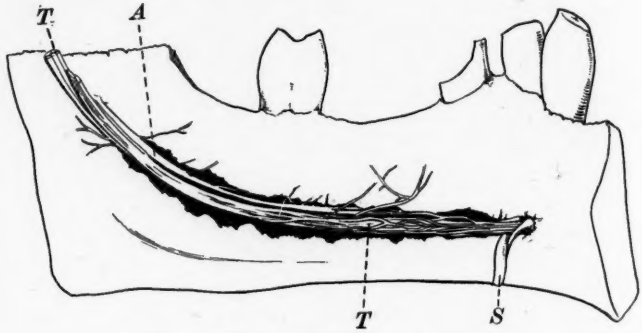

Fig. 1. Human mandible (internal aspect).

Figs. 1 and 2 are taken from a dissection of the intra-osseous course of the inferior dental nerve. In this specimen the nerve, immediately after entering the mandibular canal, divided into several branches, one of which, the alveolar branch, was separate from the rest. It ran forwards to the first premolar tooth in a plexiform manner, the "alveolar" plexus from which were given off the filaments to the molar, premolar, and possibly the canine teeth. At the premolar it divided into internal and external branches. The internal rejoined the main nerve trunk, whilst the external ran forward to supply fibres to the incisor plexus. The rest of the branches, three or four in number, ran forward for a short distance and then rejoined. This process was repeated and resulted in an increase in the number of branches, so that by the time the mental foramen was reached there were fifteen or more branches. These had a large amount of very soft connective tissue between them.

At the level of the canine tooth the majority of the fibres became enclosed in a common sheath and emerged from the mental foramen as the mental nerve. The remaining bundles were joined by the terminal fibres of the external

branch of the alveolar nerve, described above, and formed a very intricate "incisor" plexus, from which twigs ran to the periosteum and the roots of the incisor teeth.

This incisor plexus is situated on the external aspect of the jaw, and does extend posterior to the canine tooth. It is extremely complex, as fig. 2 shows, and forms a most elaborate network in this part of the jaw. Microscopic examination demonstrated quite clearly that the fibres of the incisor plexus were actual nerves.

In the posterior two-thirds of their intra-mandibular course the inferior dental nerve and vessels were surrounded by a sheath of compact bone, and a tough thick layer of connective tissue. The bony sheath disappeared more anteriorly, but the fibrous layer could still be traced along the larger branches

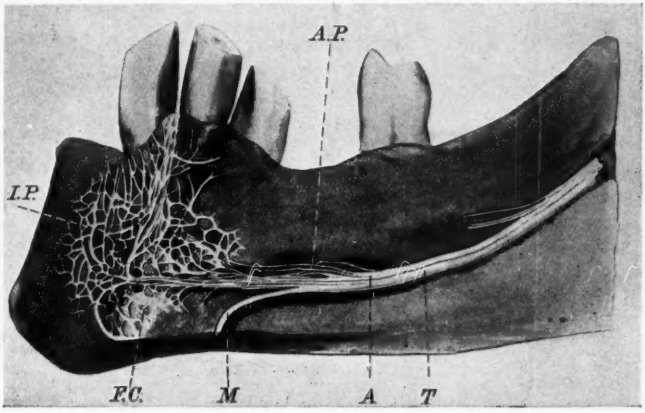

Fig. 2. Human mandible (external aspect).

of the nerve. As in Olivier's cases, the smaller branches of the nerve appeared to be without a sheath.

Four more dissections were made of the intra-mandibular course of the inferior dental nerve and showed the same features of:

(1) An alveolar branch given off early to supply the teeth posterior to the incisors.

(2) An incisor plexus.

(3) A dense fibrous sheath surrounding the nerve and vessels.

In these four specimens certain variations from the type specimen were noted. In one the nerves to the incisor teeth came off the mental nerve. The nerve supply to the canine was variable, it either came from the alveolar nerve, or the incisor plexus. The sheath of compact bone was seen in two of the specimens.

In each of the five specimens there was a part of the jaw near the root of the canine teeth which contained little or no bone, but was filled with fat (see fig. 2).

The terminations of the inferior dental nerves in the region of the symphysis were now investigated. In ten specimens which were examined, it was found that the nerves at first ran forwards with possibly a slight inclination downwards or upwards. In each case when the nerves arrived near the actual symphysis they altered their course and turned sharply upwards towards the teeth, so that the two nerves now ran more or less parallel to each other (fig. 3). In only six of the specimens was it found to be possible to make a satisfactory

Fig. 3. Human mandible (anterior aspect).

dissection of the finer branches of the nerves without damaging them. Unlike Olivier we were able on four occasions to trace distinct anastomotic fibres across the symphysis as shown in fig. 3. In the remaining two cases the most careful dissection failed to reveal any fibres connecting the one nerve with the other.

These results tally with those of Stewart and Wilson (2), who showed clinically that in many patients there was no overlap, and in those where it was present it generally did not extend beyond the central incisor and never beyond the lateral ones on the opposite side.

Dissections were made of the jaws of the cat, rabbit and sheep. In all of them a tough fibrous sheath surrounded the main nerves and its larger branches. The sheath of compact bone was only seen in the cat. All the specimens showed

the "incisor" and "alveolar" plexuses to a varying degree. The former supplied the incisor and canine teeth and the latter the remainder. No communicating fibres crossed the symphysis in any of these animals. The alveolar nerve was always present and came off from the inferior dental nerve soon after it entered the mandibular canal. This branch formed the larger part of the alveolar plexus.

SUMMARY

The paper contains an account of the intra-mandibular course of the inferior dental nerve. The following observations were made:

1. There are two definite plexuses: (*a*) a postero-internal alveolar plexus; (*b*) an antero-external incisor plexus.

2. The molars and bicuspids receive their nerve supply from the alveolar plexus, the incisors from the incisor plexus, and the canines from either of them.

3. The inferior dental nerves do not always extend across the symphysis and so overlap. If such an overlap is present it seldom extends beyond the central, and never beyond the lateral incisor teeth of the opposite side.

We have to express our thanks to Prof. Stopford for his kindness in allowing us to carry out the investigation in his department. We are also indebted to Miss Davidson for the admirable drawings with which this paper is illustrated.

ABBREVIATIONS USED IN FIGURES

A. Alveolar branch.
A.P. Alveolar plexus.
F.C. Fat cavity.
I.P. Incisor plexus.
L.I. Left incisor branch.
M. Mental branch.
R.I. Right incisor branch.
S. Fibrous sheath.
T. Main nerve trunk.

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A NOTE ON THE CENTRE MÉDIAN NUCLEUS OF LUYS

By DAVID McK. RIOCH
National Research Council Medical Fellow

From the Dutch Central Institute for Brain Research, Amsterdam, and the University Laboratory of Physiology, Oxford

The centre médian was first described by Luys, 1865, and since that time has been a well-recognised nucleus in the thalamus of primates. In lower forms, however, the homologous structure has not been clearly defined, and consequently considerable vagueness and some inaccuracies have arisen in the literature. In a study of the thalamus of *Tarsius*, Dr W. E. Le Gros Clark (1930) showed that the centre médian of Luys lay in the caudal part of the internal medullary lamina at the level of the habenulo-peduncular tract, and was medially bounded by the nucleus parafascicularis. He pointed out that a similar nucleus exists in *Tupaia* (Le Gros Clark, 1929). Dr Le Gros Clark suggested to the present author that it was probably homologous with the lateral part of the nucleus parafascicularis of the dog as described in a previous communication (Rioch, 1929). With this in mind the following brief study was made of several species of monkeys and Carnivora. The results are recorded here, as it is felt that this nucleus may have an important bearing on the phylogenetic development of sensation.

The material studied consisted of serial, transverse sections of the brains of *Cercopithecus*, *Cebus capucinus*, *Lemur catta*, *Canis familiaris* and *Felis domestica* stained by the Weigert-Pal method, and of *Phoca vitullina* stained by the Giemsa method.

The centre médian in *Cercopithecus* (fig. 1) is a relatively large, well-defined nucleus lying in the internal medullary lamina at the level of the habenulo-peduncular tract. The cells are small and are moderately densely grouped. A number of the lamellar fibres run through the nucleus, but the majority lie lateral to it, forming, as it were, a capsule around the lateral margin. This capsule separates the nucleus ventrally from the arcuate nucleus of Flechsig, laterally from the ventral nucleus and dorso-laterally from the lateral nucleus. Medially the centre médian is more or less continuous with the nucleus parafascicularis which immediately surrounds the habenulo-peduncular tract. The demarcation between the two is shown in Weigert-Pal material by a somewhat more dense grouping of the fibres of the internal medullary lamina than is found in the nucleus itself. Dorsal to the centre médian the internal medullary lamina continues between the caudal pole of the medial nucleus and the lateral nucleus. The fibres are more scattered and there are few cells lying between

them. Rostrally the centre médian is continuous with the cells forming the intralamellar nuclei (nucleus paracentralis and nucleus centralis lateralis). Caudally it is bounded by fibres between the mesencephalon and the thalamus, caudal to which again lies the posterior commissural system.

In *Cebus* (fig. 2) the relations are quite similar. The centre médian is relatively slightly smaller, the medial boundary is less well-defined and there are a greater number of fibres of the internal medullary lamina running through the nucleus.

In *Lemur* (fig. 3) the centre médian is less well-defined than in *Cebus*, especially medially. It is also relatively smaller, being only a little larger than the habenular complex. The nucleus parafascicularis, on the other hand, is larger. The arrangement of the cells is similar to that in the first two forms described, but there are considerably more fibres running through the nucleus. The topographical relations to the medial portion of the thalamus, to the epithalamus and to the arcuate nucleus of Flechsig are similar to those found in the higher monkeys, but dorso-laterally it is bounded by the pulvinar, rather than by the lateral nucleus, due to the smaller size of the lateral nuclear group of nuclei present in *Lemur*.

In the dog (fig. 4), which may be taken as a type for Carnivora, the centre médian is much less clear. The cells are more scattered than in the centre médian of monkeys, and lie amongst the fibres of the caudal portion of the internal medullary lamina which fill the nucleus. The topographical relationships with the medial portion of the thalamus, with the epithalamus and with the arcuate nucleus of Flechsig, are again entirely similar to those found in higher forms. The relationships differ, however, in the dorso-lateral portion of the thalamus, where the boundary is now formed by the nucleus supra-geniculatus and the nucleus posterior. In the cat the status is similar to that in the dog. Fig. 5 is taken from a section through the rostral pole of the nucleus, where it becomes continuous with the nucleus paracentralis.

In *Phoca vitullina* (fig. 6) the topography of this region is altered by the more dorso-lateral position of the ventral nuclear group. The centre médian is relatively larger and is more clearly defined than in Carnivora, but the relationships are otherwise similar.

von Monakow (1895) stated that his nucleus medialis b in the cat was homologous with the centre médian of Luys. This is only partially correct, as it is the more or less circumscribed, caudal portion of the nucleus medialis b in the cat which corresponds to the centre médian of higher forms. The rostral portion of the nucleus medialis b is a separate entity. Sachs (1909 *a*), in a study of the comparative anatomy of the thalamus, described the centre médian of Luys and the arcuate nucleus of Flechsig in a large number of species. He found the centre médian to be well developed in *Pitheci*, *Lepus*, *Natantia* and *Macropus*, and relatively small in *Lemur*, *Pteropus*, Carnivora, Rodentia and *Parameles*. Sachs did not differentiate the centre médian from the nucleus parafascicularis. In Winkler and Potter's atlas of the cat's brain

(1914) the centre médian is not named. It lies in the region just lateral to the nucleus of the tract of Meynert in Plates XII and XIII. Gurdjian (1927) did not describe a centre médian in the albino rat, apparently including it in the nucleus parafascicularis (*n. parafasc.* in his figure No. 7). The present writer committed the same error (the ventro-lateral portion of *n. paraf.* in Fig. 9 (Rioch, 1929)). Papez (1929) mentions the centre médian in the cat, but in his illustrations the region so designated is really a portion of the nucleus posterior.

Le Gros Clark (1930) points out the progressive phylogenetic development of the centre médian in the series *Tupaia, Tarsius, Lemur, Cercopithecus* and *Homo.* He suggests that "it may be regarded as an integrating mechanism related to the functions of that part of the thalamus in which progressive differentiation and growth are most obtrusive in higher primates." This is supported by Sachs's observation (1909 *b*) that the centre médian is mainly connected with the lateral part of the thalamus and that it has no efferent connections to the cortex. A further suggestion was made by Prof. C. U. Ariëns Kappers in a personal communication. The topographical relationship of the group formed by the centre médian and the nucleus parafascicularis to the epithalamus and the habenulo-peduncular tract in mammals is similar to that of the nucleus rotundus to the same structures in reptiles and birds, and may indicate an homology. This is contrary to the theory advanced by Ingvar (1923), who regards the mammalian ventral nucleus as homologous with the nucleus rotundus of sub-mammals, but it agrees well with the general division of the thalamus (Kappers, 1921, 1929) into a phylogenetically old, internal portion and a phylogenetically young, external portion. Thus, it may be that the centre médian differentiates out of the main diencephalic sensory centre of sub-mammals, and in such a case it would be concerned with phylogenetically old sensory functions. More evidence in the form of fibre connections, myelinated and non-myelinated, will be required for the solution of this problem.

I wish to take this opportunity of expressing my appreciation to Prof. C. U. Ariëns Kappers and Prof. W. E. Le Gros Clark for their kindness and assistance.

SUMMARY

The centre médian lies in the caudal portion of the internal medullary lamina, at the level of the habenulo-peduncular tract. Caudo-medially, especially in lower mammals, it fuses with the nucleus parafascicularis. It is probably present in all mammals, but is larger and better differentiated in the higher forms.

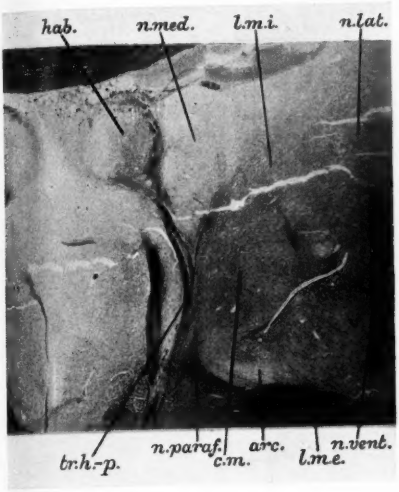

Fig. 1

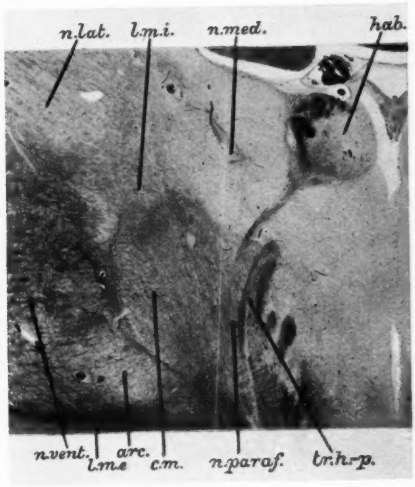

Fig. 2

Fig. 3

Fig. 4

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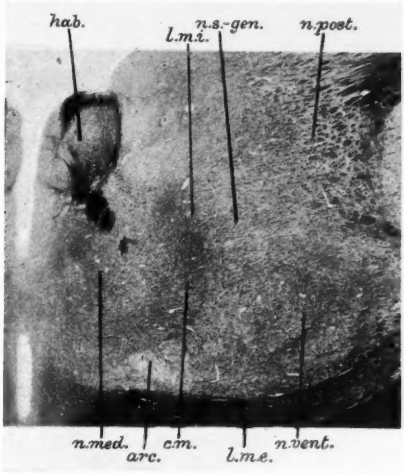
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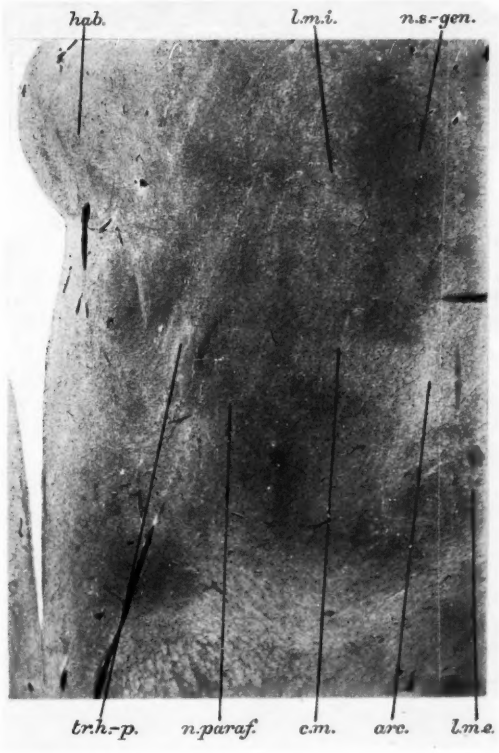
n.vent.

Fig. 5


hab.
l.m.i.
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tr.h.-p.
n.paraf.
c.m.
arc.
l.m.e.

Fig. 6

DESCRIPTION OF PLATES I AND II

Fig. 1. *Cercopithecus.* Transverse section of the thalamus at the level of the habenulo-peduncular tract. Weigert-Pal. (×7.)

Fig. 2. *Cebus capucinus.* Transverse section of the thalamus at the level of the habenulo-peduncular tract. Weigert-Pal. (×7.)

Fig. 3. *Lemur catta.* Transverse section of the thalamus at the level of the habenulo-peduncular tract. Weigert-Pal. (×7.)

Fig. 4. *Canis familiaris.* Transverse section of the thalamus at the level of the habenulo-peduncular tract. Weigert-Pal. (×7.)

Fig. 5. *Felis domestica.* Transverse section of the thalamus at a level just rostral to the main portion of the habenulo-peduncular tract. Weigert-Pal. (×7.)

Fig. 6. *Phoca vitullina.* Transverse section of the thalamus at the level of the habenulo-peduncular tract. Giemsa. (×7.)

LIST OF ABBREVIATIONS

arc.	Arcuate nucleus of Flechsig.
c.m.	Centre médian of Luys.
hab.	Habenular complex.
l.m.e.	Lamina medullaris externa.
l.m.i.	Lamina medullaris interna.
n.lat.	Nucleus lateralis.
n.med.	Nucleus medialis.
n.paraf.	Nucleus parafascicularis.
n.post.	Nucleus posterior.
n.s.-gen.	Nucleus supra-geniculatus.
n.vent.	Nucleus ventralis.
pul.	Pulvinar.
tr.h.-p.	Tractus habenulo-peduncularis.

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THE RELATIVE POSITIONS OF THE CARTILAGINOUS AND OSSEOUS TRANSMEATAL AXES IN THE HUMAN HEAD

By GEORGE G. CAMPION, L.D.S. and MATTHEW YOUNG, M.D.

Any comparison of the auricular heights of living beings with those of skulls of past ages involves an investigation of the relative positions of the cartilaginous and osseous transmeatal axes, and also of these axes to the Frankfurt plane.

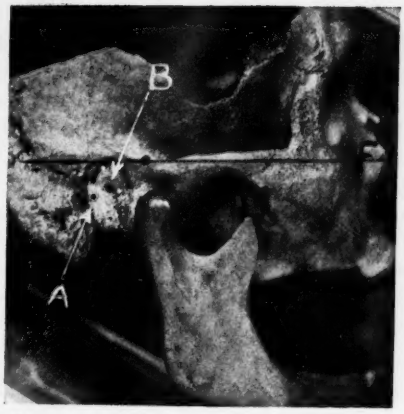
Fig. 1 shows the result of an experiment elaborated in conjunction with Sir Arthur Keith and Miss Tildesley and which through the kindness of Prof. Stopford was carried out on a subject in the dissecting room of the Manchester University. This was done with the invaluable help of Mr J. Millard, the teacher of Sculpture in the Manchester Municipal School of Art, to whom I am also indebted for the drawing shown in fig. 2.

The skull was bared on the frontal bone, zygoma and mastoid portion of temporal. A head-spanner fitted with removable wooden ear-plugs, as shown in fig. 3, was placed in position and plaster moulds made so that the ear-plugs, retained in the plaster moulds, could be again placed *in situ* after the skull had been macerated. The wooden plugs had previously had fine holes drilled axially through their points and, after maceration, the plugs and moulds thus prepared were used to insert small tubes in the skull in positions corresponding respectively with the cartilaginous and osseous meatal axes. These tubes appear as black dots in fig. 1: *A* showing the position of the cartilaginous, *B* of the osseous axis.

Subsequent measurement by Miss Tildesley with a craniophore showed that, in this case, the cartilaginous transmeatal axis had been 2·5 mm. below the osseous axis, and the photograph shows it to have been definitely posterior.

This experiment showed the technique to be unsuitable for collecting statistics of a number of cases, since it involved entire loss of the head for dissecting purposes. A different procedure was accordingly devised.

A curved quadrant (fig. 2) was made so that it could be placed in a defined position on the head-spanner, its lower border when in place being 6 mm. above the axis of the ear-plugs. The lower margin of the orbit being then found with the point of a scalpel, the quadrant enabled the body of the head-spanner to be placed approximately at right angles to the Frankfurt plane. The skin at the vertex was then marked and a strip of skin and periosteum about $\frac{3}{4}$ in. wide and 4 in. long removed transversely across the skull. This being done, the quadrant was applied a second time and the skull marked at the exact spot where the plunger of the head-spanner touched it when the lower border of the quadrant was coincident with the Frankfurt plane. A saw cut was then made at this point, the cutting edge of the saw being held parallel to the axis



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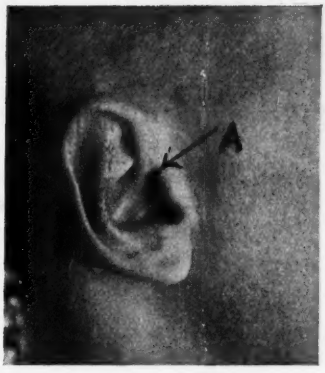

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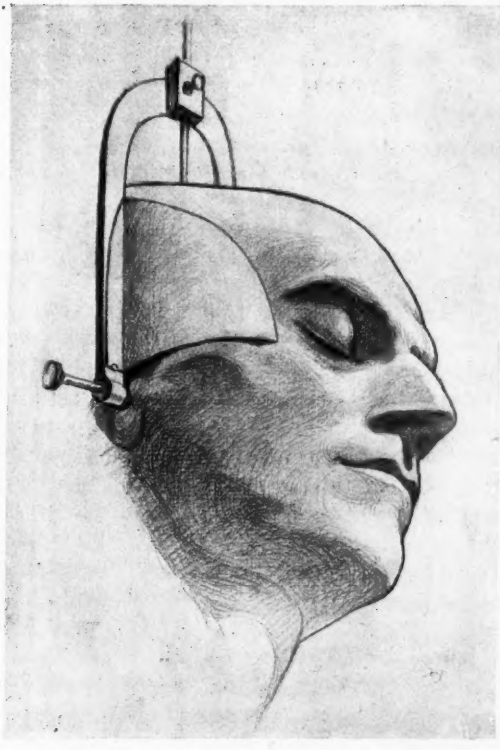

Fig. 2

of the ear-plugs. The skin and periosteum were then removed from the nasion and a cross cut made with a saw at its deepest part. A vertical incision was made through skin and periosteum at the mental point and the parts separated so that a measurement could be made there to the surface of the bone.

Fig. 3 shows a further modification of the head-spanner for the work. The usual rods and ear-plugs are removed, and rods and plugs as shown in this figure substituted. The ear-plugs, which are of wood, are fitted to slide exactly on to the brass rods. The rods are cut at one end as shown in the figure and at the other are furnished axially with a steel needle.

The arrangements here figured enable measurements to be made on the same subject:

(1) From the meatal axis (cartilaginous) to the vertex of skull.

(2) From the meatal axis (osseous) to the vertex of skull.

(3) From the Frankfurt plane to the vertex of skull. In this measurement the wooden plugs are dispensed with and the knife edge (fig. 3, *A*) used.

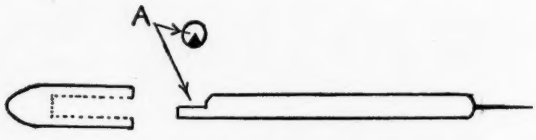

Fig. 3. Special rod and ear-plug from head-spanner. The knife edge indicated at *A* is used to measure from the Frankfurt plane to vertex.

(4) From the supra-tragal notch as indicated in fig. 4 to the vertex. For this measurement the rods in the head-spanner are reversed and the needle inserted through the skin into the cartilage at the spot marked *A* in fig. 4. This measurement was made in the later cases in the series as a means of investigating the relationship of the centre of the supra-tragal notch to the Frankfurt plane.

After the measurements *A*, *B*, *C*, *D* and *J* in Table I have been made, an incision is made at the reflection of the skin from the dorsum of the ear to the occiput, the ear turned forward and the cartilaginous meatus entirely removed from the osseous meatus. Next the measurements *E*, *F*, *G*, *H*, are made using the ear-plugs in the osseous meatus: then measurement *K* without the wooden ear-plugs, and finally the sagittal measurements *L*, *M*, *N*.

The results of a number of observations extending over 2 years are shown in Table I.

Selecting from Table I the figures in columns *A*, *E*, *K*, for comparing the relative heights of (1) Frankfurt plane, (2) osseous axis, (3) cartilaginous axis, we find these compared in Table II.

The figures obtained in thirty-six cases of male subjects by the method here set out, which have been treated statistically by Dr Matthew Young,

show as follows in the essential points for which the investigation was undertaken.

	Frankfurt plane to centre of osseous axis	Frankfurt plane to centre of cartilaginous axis	Osseous axis above cartilaginous axis
Means (mm.) and standard errors ...	5·63 ± 0·18	8·26 ± 0·35	2·63 ± 0·39
Coefficient of variation (%)	18·65 ± 2·27	25·18 ± 3·15	84·79 ± 15·60
Range of variation (mm.)	3·5 to 8	5·3 to 14·5	− 1 to 8·5

I wish to express my indebtedness and thanks to Prof. Stopford for the facilities granted for this investigation and to the following gentlemen for most valuable help in making and checking the measurements in the dissecting room: Messrs L. G. Campion, J. N. Peacock, R. Bradbury, R. G. Dawson, R. Cocker, J. D. Evans, and D. R. Dickson.

G.G.C.

The results that may be deduced from the figures in Tables I and II may be stated very briefly. In the thirty-six male subjects, the osseous axis lies, on the average, 2·63 ± 0·39 mm. higher than the cartilaginous axis. This difference in the mean distances of the two axes from the Frankfurt plane may be considered statistically significant as it exceeds twice its standard error. The variability in the difference is very considerable, however, as is shown by a coefficient of variation of 85 per cent., and it is evident that great caution must be exercised in drawing inferences as to the relative auricular heights when comparing measurements of this dimension in living people and skulls. The distance from the cartilaginous axis to the Frankfurt plane would appear to be slightly more variable than the distance from the osseous axis to the same level but the apparent difference in variability cannot be considered significant.

In Table I, there are only fourteen subjects in which measurements from the supra-tragal notch to the vertex are recorded. On comparing these measurements with the values of the distance from the Frankfurt plane to the vertex in the corresponding cases, it is found that the notch varies in its position with respect to the plane from 1 mm. below to 3·7 mm. above, and, that, on the average, it lies 1·27 ± 0·35 mm. above the plane. Though the number of observations is too small to warrant any emphasis being laid on the actual value, the data seem to indicate that the notch lies at a slightly higher level than the Frankfurt plane.

Table I supplies also figures from which may be determined the relative distances of the cartilaginous and osseous axes from the nasion and mental point respectively. In thirty-six cases the mean distance of the cartilaginous axis from the nasion is 96·32 ± 0·63 mm. and the mean distance of the osseous axis from the same point 95·48 ± 0·54 mm. The difference in these mean values is 0·84 ± 0·83 mm., which cannot be considered significant. In twenty-eight cases the mean distances of the cartilaginous and osseous axes from the mental point are 116·93 ± 1·54 mm. and 119·06 ± 1·56 mm. respectively. The difference between these means is 2·13 ± 2·19 mm., a value to which, as in the previous case, no significance can be attached in view of the size of its standard error.

M.Y.

Table I

Serial no.	Date	Sex	Cart. axis to vertex *A*	Cart. axis to nasion *B*	Cart. axis to upper incisors *C*	Cart. axis to mental point *D*	Oss. axis to vertex *E*	Oss. axis to nasion *F*	Oss. axis to upper incisors *G*	Oss. axis to mental point *H*	Supra-tragal notch to vertex *J*	Frankfurt plane to vertex *K*	Vertex to nasion *L*	Nasion to upper incisors *M*	Nasion to mental point *N*
1	iv. 28	M.	125	96	100	—	122	91·5	—	—	—	115	—	—	—
2	„	„	123	98	—	—	117	95	—	—	—	111	124	—	—
3	„	„	136	102	—	—	128	100	—	—	—	121·5	136·5	—	—
4	„	„	124·5	101	—	—	120	98·5	—	—	—	114·5	—	—	—
5	„	„	118·5	92·5	—	—	116	93·5	—	—	—	109·5	114	—	—
6	„	„	111	88	—	—	111	90·5	—	—	—	105	108	—	—
7	„	„	122	95	—	—	121·5	94	—	—	—	114·5	123·5	—	—
8	„	„	128	102·5	—	—	119·5	92·5	—	—	—	114·5	—	—	—
9	3. x. 28	„	132·5	99	—	113	129	98	—	115	—	124	132	—	122
10	„	„	127	102	—	114	123·5	102	—	120	—	119	121	—	139
11	„	„	121	95·5	—	110	115	94	—	115	—	111·5	119	—	126
12	„	„	131	99	—	110	126·5	96·5	—	111·5	—	119·5	128	—	133
13	„	„	126	95	—	117	127	96·5	—	117	—	120·5	125	—	119·5
14	„	„	129	103·5	—	122	127·5	104	—	123·5	—	122	130·5	—	125
15	„	„	135	96·5	—	136	133·5	96·5	—	140	—	127	127·5	—	132
16	„	„	124·5	96·5	—	140	122·5	95·5	—	141	—	117·5	118	—	134·5
17	22. iv. 29	„	122	88	96	107	118	90·5	102	113	—	113·5	122	73	111·5
18	„	„	122	96	—	117	120	95·5	—	117	—	114	118	—	132·5
19	„	„	128	97	—	123	126	95	—	125·5	—	120	120	—	137
20	„	„	123	95	—	120	120·5	96·5	—	123	—	115	127·5	—	120·5
21	„	„	124	96·5	109·5	122·5	124·5	93	106	119	—	118	124	79	122
22	21. v. 29	„	127·5	96·5	—	114	122·8	95	—	116	—	118	119·5	—	126
23	2. x. 29	„	119·3	93·5	98	111·8	118·3	93·5	100	114	112·5	112·8	117·5	79	127
24	„	„	120	94	103	119·5	117·5	94·5	106	123	111·3	112	118·5	78·5	122·5
25	„	„	127·8	96·3	—	100·5	126·3	94	—	102	121·5	121·8	121·5	—	124
26	„	„	129·5	94	109	117·3	126	93·5	111·3	121	120	121·5	132·5	79	132·8
27	„	„	121·5	100·5	—	115·5	120	100·5	—	117·3	113·5	115·3	118·5	—	137·3
28	„	„	119·3	88	—	111	117·8	88·5	—	114	111	110	114	—	113·5
29	„	„	127·3	95·8	95·5	118·8	128	95·5	97	120	120	122	122	81	138·5
30	23. iv. 30	„	127·5	98	—	112·8	124	94	—	115	117	119	129	—	135
31	„	„	129	91·5	—	116·5	126	93·5	—	110	120·5	122	124·5	—	127·5
32	„	„	134·5	101	—	124	130	99·8	—	129	126·5	126	132·5	—	138
33	„	„	130	95·5	—	106	130	95·5	—	110	122	122	126	—	131
34	„	„	121	97	—	112	118·5	98	—	116	110·5	113	121·5	—	134
35	„	„	131	93·5	106·5	116·5	130·5	93·5	107	117	121·8	125·5	129	87	133
36	„	„	128	97·8	—	126·3	128	99	—	129	118	121	124·5	—	146·8
37	iv. 28	F.	119·5	88·5	—	—	110	84	—	—	—	104·5	115	—	—
38	„	„	114	90	—	—	113	89·5	—	—	—	108	—	—	—
39	„	„	120·5	90	—	—	116·5	87	—	—	—	110·5	—	—	—
40	„	„	129·5	—	—	—	127	—	—	—	—	120	—	—	—
41	22. iv. 29	„	124·5	93·5	—	102·5	124	94	—	104·5	—	117	125	—	113

Table II

Serial no.	Cart. axis to vertex *A*	Oss. axis to vertex *E*	Frankfurt plane to vertex *K*	Frankfurt plane to centre of oss. axis	Frankfurt plane to centre of cart. axis	Oss. axis above cart. axis
1	125	122	115	7	10	3
2	123	117	111	6	12	6
3	136	128	121·5	6·5	14·5	8
4	124·5	120	114·5	5·5	10	4·5
5	118·5	116	109·5	6·5	9	2·5
6	111	111	105	6	6	0
7	122	121	114·5	6·5	7·5	1
8	128	119·5	114·5	5	13·5	8·5
9	132·5	129	124	5	8·5	3·5
10	127	123·5	119	4·5	8	3·5
11	121	115	111·5	3·5	9·5	6·0
12	131	126·5	119·5	7	11·5	4·5
13	126	127	120·5	6·5	5·5	−1
14	129	127·5	122	5·5	7	1·5
15	135	133·5	127	6·5	8	1·5
16	124·5	122·5	117·5	5	7	2
17	122	118	113·5	4·5	8·5	4
18	122	120	114	6	8	2
19	128	126	120	6	8	2
20	123	120·5	115	5·5	8	2·5
21	124	124·5	118	6·5	6	−0·5
22	127·5	122·8	118	4·8	9·5	4·7
23	119·3	118·3	112·8	5·5	6·5	1
24	120	117·5	112	5·5	8	2·5
25	127·8	126·3	121·8	4·5	6	1·5
26	129·5	126	121·5	4·5	8	3·5
27	121·5	120	115·3	4·8	6·3	1·5
28	119·3	117·8	110	7·8	9·3	1·5
29	127·3	128	122	6	5·2	−0·8
30	127·5	124	119	5	8·5	3·5
31	129	126	122	4	7	3
32	134·5	130	126	4	8·5	4·5
33	130	130	122	8	8	0
34	121	118·5	113	5·5	8	2·5
35	131	130·5	125·5	5·0	5·5	0·5
36	128	128	121	7·0	7·0	0

PRELIMINARY NOTE ON MAMMALIAN LYMPHOID TISSUE AND ITS RELATION TO THE REMAINDER OF THE HAEMOPOIETIC SYSTEM

By J. M. YOFFEY, M.Sc., M.D. (Manch.)

Assistant Lecturer in the Department of Anatomy at the University of Manchester

The present work was suggested by the results of an investigation which had been previously conducted into the histology and physiology of the spleen in fishes (1). It was found that in fishes the various formed elements of the blood developed from one common ancestral cell, which resembled very closely the small round cell or lymphocyte of higher vertebrates.

In the dogfish, which affords a typical example of haemopoiesis in fishes, the development of the lymphocyte into the mature blood cell takes place in two stages. The first stage occurs in the spleen, where the lymphocyte acquires a thin coating of specialised cytoplasm and develops into a young erythrocyte or granulocyte. This is then swept into the blood stream, where it undergoes the second and final stage of its development. In mammals the final stages in the maturation of the blood cells occur under normal conditions in the bone marrow. In the various collections of lymphoid tissue there is usually no obvious formation of either erythrocytes or granulocytes. Certain observers have described such formation as occurring, but the significance of their work has never been fully appreciated.

Jordan (2, 3, 4) has described in mammals numerous isolated instances of the development of erythrocytes in lymphoid tissue. Maximow (5, 6, 7, 8), on the other hand, by the methods of tissue culture, has shown that under the artificial conditions present in cultures lymphocytes can develop into both erythrocytes and granulocytes.

But if lymphoid tissue possesses the same haemopoietic function in mammals as in fishes, one of two things must be assumed. Either the few lymphocytes in the bone-marrow are the source of all the cells in the blood, or else an additional stage or stages are introduced into the haemopoietic cycle. According to the latter assumption, lymphocytes would first be formed in the scattered nodules of lymphoid tissue, where they might undergo the earliest stages of their differentiation, without as a rule giving any indication of the type of cell into which they were evolving. Secondly, they would pass into the blood stream, where they might undergo a further portion of their development, or might merely be in transit for the third stage, their maturation in the bone-marrow. From the bone-marrow they would finally pass back again into the blood stream, in which they remain until destroyed.

Such a scheme of development contains an element of hypothesis. This hypothesis does not lie in the view that lymphocytes can develop into erythrocytes or granulocytes, for the work of numerous observers has placed this fact beyond all possible doubt. What is hypothetical, however, is the idea that the blood stream normally conveys cellular elements from one tissue to deposit them in another, so that in the present instance the blood would convey cells from the lymphoid tissue to the bone-marrow.

It is well known, of course, that the blood performs such a function in the case of certain chemical substances, the group of hormones. Under certain pathological conditions also we know that cellular elements may be carried by the blood stream from one part of the body to another—the so-called haematogenous metastases of new growths. But in the latter instance there are obvious gross mechanical factors at work, viz. the erosion of the vessel wall by portions of the new growth which project into the lumen and are thereupon swept into the blood stream; whereas the transference of single cells, as a regular phenomenon occurring under normal conditions, has yet to be proved.

OUR PRESENT KNOWLEDGE OF LYMPHOID TISSUE

It is very instructive to analyse the present state of our knowledge concerning lymphoid tissue. We know that under certain pathological conditions lymph nodes are particularly prone to become involved, and that in bacterial infections they may filter off bacteria and prevent them from entering the blood stream. But in this connection one must observe that the lymphatic *vessels* actually facilitate the spread of infection and malignant disease. In any case the main function of lymphoid tissue, under normal conditions, seems to be to contribute lymphocytes to the blood.

It is generally assumed that all lymph nodes are functionally equal, and that there is no great difference, for example, between an inguinal, an axillary, and a mesenteric lymph node. Yet it is clear that as between the mesenteric and the non-mesenteric nodes there are important circulatory and metabolic differences. Under normal conditions the greater portion of the lymph entering the thoracic duct comes from the intestinal villi, passing en route through the mesenteric nodes. Through the non-mesenteric nodes the lymph circulation is ordinarily almost negligible, but increases during exercise. The intestinal lymph conveys to the mesenteric nodes some of the products of digestion, as far as we know chiefly fats and lipoids. The lymph passing through the non-mesenteric nodes, especially when it is passing most freely (during exercise), conveys almost entirely waste products of metabolism. It would therefore appear probable, *a priori*, that these differences in the constitution and flow of lymph would be associated with differences in reaction and development on the part of the cells with which the lymph comes into contact.

The mesenteric nodes occupy towards the intestine much the same position with reference to the flow of lymph as the liver with reference to the flow of blood. Blood leaving the intestines, and containing various digestive products, passes first of all to the liver. The liver has first choice of the products of digestion, and picks out from the blood of the portal vein such elements as it requires, the blood then passing via the hepatic veins into the general circulation, conveying into the blood stream the special products of hepatic activity.

The mesenteric nodes are situated in precisely a similar position with reference to the lymph circulation. The idea therefore of a similarity in functional relationship possesses a definite anatomical basis. It is indeed a striking

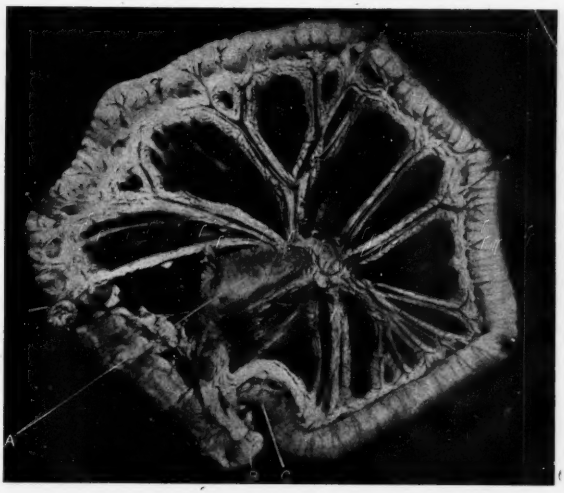

Fig. 1. Photograph of distal portion of small intestine and commencement of large intestine of a cat, injected with carmine gelatine.

A=Glandula mesenterica magna. The various branches of the superior mesenteric artery and vein all pass through this gland. The intestinal lymphatics all enter it, but cannot be seen clearly in the photograph.

B=Caecum.

C=Termination of small intestine, just before opening into caecum.

phenomenon to observe, in the mesentery of the cat or dog, the numerous lymph vessels all converging to the large mesenteric node. This lymph node (or collection of nodes) is of remarkably large size as compared with lymph nodes elsewhere, and has in consequence been specially named the "glandula mesenterica magna," or "pancreas Asellii" (fig. 1).

The name glandula mesenterica magna is particularly appropriate in the dog, where the actual bulk of mesenteric lymphoid tissue is very considerable. In many cases it is larger, in point of its cellular elements, than the spleen (that is, of course, the empty spleen). In this connection it must be pointed

out that the total amount of lymphoid tissue in the body must be very considerable, and it is only its diffuseness of distribution which obscures this fact. When one takes into account the various nodules associated with the wall of the alimentary tract, the pharyngeal lingual and palatine tonsils, Peyer's patches and the solitary lymph nodules in the intestine, the lymph nodes of the mesentery, and those at the root of the limbs as also the lymph nodes of the head and neck, it is clear that the total mass of lymphoid tissue, if collected together, would form an organ of no inconsiderable size. Yet to this large cellular aggregate we are able to assign very little in the way of normal functioning. The one function which we can definitely allot is the formation of lymphocytes and their discharge into the blood stream.

The entry of lymphocytes into the blood stream raises however an obvious question. What is the further history of the lymphocytes once they have entered the circulation? A dead cytological remnant like the erythrocyte is finally destroyed by the wear and tear of repeated circulation, and the broken down fragments or whole cells on the verge of disintegration may be found circulating, or ingested by phagocytic cells in certain localities. But the lymphocyte, unlike the erythrocyte, is a living nucleated cell, and there is no evidence of its destruction in this manner. Consequently we find ourselves faced with a curious phenomenon. The lymphocytes in the blood are not broken down by mechanical means or destroyed by phagocytosis; yet their numbers remain constant, in spite of the fact that many new ones are being continually introduced. One is therefore driven to the conclusion that while some lymphocytes are entering the blood stream, others are leaving it. And the number of lymphocytes in the blood at any moment is the result of a balance between these two processes. The term lymphocytosis is therefore a relative term and does not always possess the same significance. It might on the one hand be due to increased entry of lymphocytes into the blood stream; on the other hand it might be due to diminished withdrawal. Some figures quoted from Heidenhain by Jordan (9) are very interesting. "In a 10-kilo dog Heidenhain estimated the number of mononuclear leucocytes daily poured into the blood from the thoracic duct at 12,800,000,000, or over three times the normal blood content. On the same basis, the number of lymphocytes which daily enter the blood-stream in man would be approximately 20,000,000,000."

This might be explained away by a theory of partial circulation of lymphocytes back again from the blood into the lymph; but it does not seem probable that this could be very extensive. That lymphocytes should continually pass from lymphoid tissue into the blood, and from the blood back again to lymphoid tissue, does not appear to subserve any useful function, in fact no function whatever. It would appear more likely that lymphocytes, once they have left the parent lymphoid tissue, proceed elsewhere.

But if lymphocytes are continually leaving the circulation, a further question arises. In what part do they leave it? Some may enter the connective

tissues in various parts of the body, forming the group of so-called histiogenous lymphocytes. But apart from lymphoid tissue proper the largest concentration of lymphoid elements to be found elsewhere is in the bone-marrow. In the bone-marrow the lymphocytes are found loosely scattered, without any organised distribution such as is found in the lymph nodes.

It may further be noted that the circulatory conditions which prevail in bone-marrow are well adapted for permitting such a transference of lymphocytes to take place. It has long been realised that the sluggish flow of blood in bone-marrow, with the periodic opening up and closing down of capillaries, is very favourable to the passage of cells from the bone-marrow into the blood. But it does not seem to have been realised that these conditions are equally favourable to the passage of cells in the reverse direction, from the blood into the bone-marrow.

It is, of course, a possibility that the lymphocytes present in bone-marrow may multiply locally and not be in need of replenishment from extraneous sources. But even here what evidence there is seems definitely to indicate that the main site of multiplication of lymphocytes is in the germinal centres of lymphoid tissue, whereas in the bone-marrow itself the multiplication of lymphocytes would appear to be almost negligible. Dividing lymphocytes are encountered in the bone-marrow with relative rarity.

In so far then as our present knowledge of lymphoid tissue is concerned, the evidence, both anatomical and physiological, would seem to incline towards some transference of cellular elements from lymphoid tissue to bone-marrow. This view has constituted the working hypothesis upon which the present researches have been based.

SUMMARY

1. The present paper is an attempt to interpret some of the known facts concerning mammalian lymphoid tissue.

2. It appears probable that cells from lymphoid tissue travel *via* the blood stream to the bone-marrow.

3. It is proposed to submit the evidence for this in subsequent papers.

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THE CONDUCTING SYSTEM OF THE MONOTREME HEART

By FRANCIS DAVIES, M.D. (Lond.)
Anatomy Department, King's College, London

INTRODUCTION

Keith, Mackenzie and Robertson (1, 2) after an extensive investigation of the hearts of vertebrates, decided that birds are unique amongst higher vertebrates in that the avian right auricle is connected to the right ventricle by multiple muscular strands not of a markedly specialised type, and these authors concluded that the auriculo-ventricular bundle, in the form of a specialised strand, is peculiar to mammals. Keith and Mackenzie admitted that the condition in the avian heart greatly puzzled them, and examined the heart of *Echidna* in the hope of obtaining a clue to their conception of the avian auriculo-ventricular connections. However, in the heart of *Echidna* they found (1, 3) a large and typical auriculo-ventricular bundle, like that in the hearts of ungulates. In addition they noted considerable remnants of the extensive auriculo-ventricular connection which prevails in lower vertebrate hearts, especially round the right auriculo-ventricular orifice, where they found a leash of fibres descending direct from the auriculo-ventricular node to the septal wall of the right ventricle. This leash they regarded as a remnant of the complete circle of inner ventricular fibres of the lower vertebrate heart. They also noted a connection, consisting of ordinary cardiac muscle, between the left auricle and left ventricle in the heart of *Echidna*. The present writer (4, 5) drew attention to the fact that in the avian heart the main auriculo-ventricular connection takes the form of a well-defined auriculo-ventricular bundle, consisting of specialised muscle, which descends from the auriculo-ventricular node into the depth of the ventricular septum and there divides into right and left limbs for distribution to the respective ventricles. Other auriculo-ventricular connections noted in the avian heart were those between the auricular and ventricular myocardial components of the muscular right auriculo-ventricular valve by means of the right auriculo-ventricular Purkinje ring. The present study (commenced at University College, London, and completed at King's College) consists of the histological examination of the hearts of *Platypus* (one) and *Echidna* (two), for which material I wish to express my gratitude to my former chief, Prof. J. P. Hill.

The specialised connections of the monotreme heart, as determined in the present work, are described below. The remarks apply equally to *Platypus* and *Echidna*, but any particular differences are mentioned. Further, the sinu-auricular and auriculo-ventricular connections thus determined are compared

with those in the placental mammalian, avian and lower vertebrate hearts, and the bearing is discussed which the condition in the monotreme heart has upon the significance of the arrangement of the specialised muscle in these other hearts.

PRESENT WORK

The sinu-auricular node

The three caval openings in the right auricle, right and left anterior, and posterior are surrounded by the right and left sinus valves. Between the left sinus valve and the inter-auricular septum is a well-defined region of the right auricle, *the intersepto-valvular space* (Plate I, fig. 1). Running upwards in the base of the right sinus valve and continued on to the roof of the right auricle is a muscular band, the crista terminalis. Beneath the epicardium, on the auricular side of the crista terminalis, is the sinu-auricular node (Plate I, fig. 2). It is ovoid in shape and tapers off above and below. It is situated mainly in relation to the crista on the roof of the right auricle, but also extends caudally in relation to about the upper half of the right sinus valve. In size it is relatively more massive than the sinu-auricular node of the hearts of placental mammals. Its specialised cells are arranged in interlacing strands with much connective tissue interspersed. The cells vary in size, some being almost as large as the ordinary auricular myocardial cells, though most are smaller (Plate I, fig. 3). Longitudinal myofibrillae are scarce and are limited to the extreme periphery of the cell, the wide perinuclear zone being clear and devoid of fibrillae. Transverse striation is not perceptible in the fibrillae. The nuclei are round or slightly oval and centrally situated; two nuclei can frequently be seen in the same cell in one section. These specialised cells of the sinu-auricular node pass into direct continuity with the neighbouring myocardial cells of the right auricle on the one hand, and on the other they merge with the myocardial cells of the cardiac end of the right anterior vena cava. The cephalic part of the sinu-auricular node is situated beneath the epicardium on the auricular (ventral) side of the crista terminalis. It is only the caudal, narrower part of the node which lies actually in the base of the right sinus valve and crista terminalis. There is no evidence of specialised nodal cells in relation to the left sinus valve in *Platypus* or *Echidna*. The arterial arrangement in relation to the monotreme sinu-auricular node differs in *Platypus* and *Echidna*. In *Platypus* (Plate I, fig. 3) the arrangement is similar to that in the sinu-auricular node of the bird and of the placental mammal in that two small arteries run longitudinally through the node and communicate by two or three branches in the node. In *Echidna* (Plate I, fig. 4) the outstanding feature is the extreme vascularity of the node, the nodal arteries being large and communicating very freely with each other. Many nerve fibres run into the sinu-auricular node from neighbouring nerve ganglia, and moreover a number of nerve cells lie actually in the node in both *Platypus* and *Echidna* (Plate II, fig. 5). Keith and Mackenzie (1) also noted

the presence of nerve cells in the sinu-auricular node in *Echidna*. In the hearts of placental mammals Meiklejohn (6) found nerve cells in the perinodal connective tissue only and not amongst the specialised nodal tissue. These details of the sinu-auricular node in the monotreme heart are of interest in considering the nature of the node in the heart of the higher mammal and bird and its relation to the sinu-auricular junctional tissues in piscine and lower reptilian hearts. It is commonly thought that the limitation of specialised nodal tissue in the higher mammalian heart to the base of the right sinus valve represents a reduction of the sinu-auricular ring of the lower reptile and the fish, and it is suggested by Mackenzie (7) and by Walmsley (8) that this reduction occurs *pari passu* with, and is caused by, the fusion of the left sinus valve with the inter-auricular septum, with consequent obliteration of the intersepto-valvular space and disappearance of the left part of the sinu-auricular ring. But, as described above, in the monotreme heart the sinu-auricular node is confined to the region of the right sinus valve (and crista terminalis) and the intersepto-valvular space is a well-defined region of the right auricle, between the left sinus valve and the inter-auricular septum. The obliteration of the intersepto-valvular space which occurs in the hearts of higher mammals cannot therefore be the prime factor in the reduction of the sinu-auricular ring of the lower vertebrate heart.

With regard to the position of the sinu-auricular node, A. Oppenheimer and B. S. Oppenheimer (9) described the node in the young human heart as lying on the venous side of the right sinus valve. Stiénon (10) from his study of foetal hearts of the rabbit, sheep and man, pushes the origin of the sinu-auricular node back to the cavo-sinus junction, while Shaner (11) finds that the sinu-auricular node in the foetal calf heart appears at the 100 mm. stage just above the cavo-atrial junction, and only just before birth sinks into the sulcus terminalis. In the adult monotreme heart, the cephalic part of the sinu-auricular node lies on the auricular side of the crista terminalis, only the caudal part lying actually in the base of the right sinus valve.

Purkinje fibres in the auricles

Much controversy has taken place concerning the presence of Purkinje fibres in the auricles in higher mammals. Keith, Flack and Mackenzie do not refer to them in their investigations. Koch (12) denies the presence of Purkinje fibres in the auricles of young human subjects and Monckeberg (13) considers that when present they are abnormal formations. Holmes (14) described Purkinje fibres in the right auricle of the calf heart, a small clump of Purkinje fibres lying near the superior vena cava and another in the musculi pectinati in the roof of the right auricle. Through the courtesy of Dr Holmes the present writer has seen his sections and has no hesitation in agreeing that the fibres he describes have all the characters of Purkinje fibres. Holmes was unable to find any Purkinje fibres in the auricles of any other mammalian heart he examined (sheep, ox, lamb, pig, camel, gazelle, human adult and child).

Tandler (15) noted the presence of Purkinje fibres in the human right auricle in the adult only. Walmsley (8) quotes Pace and Schwartz as finding Purkinje fibres in the auricles of many mammals, and Walmsley himself finds fibres agreeing in all respects with the ventricular Purkinje fibres in the following regions of the right auricle of the adult human heart: near the auriculo-ventricular node, though he is uncertain whether they are continuous with the node; at the lateral margin of the orifice of the inferior vena cava; round the orifice of the coronary sinus; and along the junction of the inter-auricular septum with the posterior wall of the right auricle.

It is noteworthy that the situations in which these Purkinje fibres have been described by the above workers are very variable, and moreover the fibres appear to form isolated strands, unconnected with the sinu-auricular or auriculo-ventricular node or with the ventricular Purkinje system. Thorel (16) described a connection between the sinu-auricular and auriculo-ventricular nodes consisting of specialised cardiac muscle, but this has not been confirmed by subsequent investigators. Todd and van der Stricht (17, 18) have gone to an extreme and state that in the adult human heart the Purkinje fibres form a network permeating the right (and probably the left) auricle just as fully as they do the ventricles. These authors concentrated their studies upon the right auricle and do not speak with the same certainty in the case of the left auricle. They also deny the right of the sinu-auricular and auriculo-ventricular nodes for special consideration, as they maintain that they are structurally identical with, and are non-specialised parts of, the general cardiac Purkinje system. The present writer (4) observed that in the bird's heart the Purkinje fibres in the right and left auricles formed a continuous system, both beneath the endocardium and around the coronary arteries in the myocardium. This avian auricular Purkinje system was found to be continuous on the one hand with the sinu-auricular node and on the other with the ordinary auricular myocardium; it was not directly continuous with the ventricular Purkinje system.

In view of the varying opinions concerning the presence and extent of distribution of Purkinje fibres in the auricles of placental mammals, the condition in the monotreme heart assumes special importance. In the present work no Purkinje fibres were found in either auricle of the Platypus heart, nor in those of one of the *Echidna* hearts examined. In the second *Echidna* heart studied, numerous cells were seen in the walls of both auricles having characters somewhat akin to those of Purkinje fibres (Plate II, figs. 6 and 7). These cells were most numerous in, and constituted the major thickness of the pectinate muscles of the left auricular appendix. They presented the following characters. Their transverse diameter averaged 12 μ, as compared with that of the auricular cells with more typical myocardial structure, which (in this particular heart of *Echidna*) had a diameter of about 10 μ. They contained two (occasionally three) nuclei, which were slightly oval in shape and central in position. The nuclei exhibited much basiphil chromatin material. About the nuclei there was a fairly wide zone devoid of longitudinal myo-

fibrillae, which were limited to the periphery of the cells. Transverse striation in these fibrillae was very distinct. The size of the cells, the very distinct transverse striation and the abundance of chromatin in the nuclei are evidence against considering these cells as Purkinje cells, although they are certainly different from the auricular muscle in the other *Echidna* heart and in the *Platypus* heart, and from the rest of the auricular musculature in this particular heart. They are of interest in relation to the description by Todd and van der Stricht (17, 18) of various types of Purkinje fibres in the heart of man. The present writer is not disposed to regard these fibres as Purkinje fibres. Their appearance does not suggest any pathological process known to the writer, nor does any improper fixation or peculiarity of staining appear to have had any action in the production of the microscopic appearance of these cells, which extend throughout the thickness of the auricular wall, and there is no suggestion of any sub-endocardial collection of definite Purkinje fibres in either auricle.

The specialised connection between auricles and ventricles

The only connection, of specialised structure, between the auricles and ventricles that could be made out in the present study was by means of the auriculo-ventricular node and its prolongations to the ventricles.

The auriculo-ventricular node
(Plate II, figs. 8 and 9)

In the heart of *Platypus* the auriculo-ventricular node lies mainly on the right side of the upper and posterior part of the cartilago cordis and partly in the lower border of the inter-auricular septum. In the two hearts of *Echidna* examined there was no cartilago cordis, but the auriculo-ventricular node occupied a corresponding site in relation to the trigonum fibrosum and to the inter-auricular septum. The auriculo-ventricular node in both *Platypus* and *Echidna* is a relatively massive structure. Its fibres resemble those of the sinu-auricular node in that they are smaller than the myocardial fibres and form a network by intercrossing in various directions, but there is not much connective tissue between the strands. Two rounded central nuclei are frequently seen in one cell, but the perinuclear clear zone is narrower and the peripheral zone exhibiting longitudinal myofibrillae is broader than the corresponding zones of the sinu-auricular nodal fibres. Transverse striation is not perceptible in the longitudinal myofibrillae. The dorsicephalic part of the auriculo-ventricular node in the *Platypus* heart is flattened transversely and its left surface is concave in adaptation to the convex right surface of the cartilago cordis, with which it lies in intimate contact. The fibres of this part of the node are continuous above and behind with the myocardial fibres of the inter-auricular septum. The ventrocaudal part of the node is ovoid in shape and is continued ventrally into the auriculo-ventricular bundle. The caudal part of the node is prolonged downwards for a short distance beneath the endocardium

on the right side of the ventricular septum at its posterior part. The fibres of this prolongation are similar in character to those of the main part of the node. They are smaller than the myocardial fibres of the ventricular septum and are quite unlike the very large Purkinje fibres of the auriculo-ventricular bundle. These nodal fibres become continuous with the superficial myocardial fibres of the ventricular septum. This prolongation of nodal fibres was noted by Keith and Mackenzie (1) in the heart of *Echidna*, and these authors also observed a similar prolongation of nodal fibres to the septal musculature in the heart of the rat. Wray Lloyd (19) describes a prolongation of specialised fibres in the rabbit heart which arises from the junction of the auriculo-ventricular node and auriculo-ventricular bundle and passes downwards beneath the attached border of the septal cusp of the tricuspid valve to become continuous with the myocardium of the ventricular septum. A similar nodal prolongation was observed (macroscopically) by Curran (20) in the heart of the calf (Plate II, fig. 10). It may be profitable here to repeat the warning, expressed by Wray Lloyd, that this septal prolongation of the auriculo-ventricular node must be borne in mind in experimental work on the conducting system of the higher mammalian heart.

No nerve cells are seen in the auriculo-ventricular node itself, but a number of nerve fibres pass into the node from nerve cells which are situated in the lower part of the inter-auricular septum. With regard to the position of the auriculo-ventricular node in relation to the sinus valves, in both *Platypus* and *Echidna* the node lies outside the region of the sinus valves. Walmsley (8) is of the opinion that in the human heart the auriculo-ventricular node lies in the proper atrial region, that is, outside the area enclosed by the sinus valves, and that therefore the auriculo-ventricular node is a derivative of the auriculo-ventricular ring of lower reptilian and piscine hearts. Mackenzie (7), on the other hand, believes that the auriculo-ventricular node is a derivative of the sinu-auricular ring of the lower vertebrate heart, and states that in the kangaroo heart the auriculo-ventricular node lies within the limits of the sinus valves. The view favoured by Mackenzie therefore is that the sinu-auricular and auriculo-ventricular nodes are right and left derivatives of the primitive sinu-auricular ring. Experimental evidence that is considered to support this view is that the right vagus and right sympathetic nerves are associated with the sinu-auricular node, while the left vagus and left sympathetic influence the auriculo-ventricular node. The present work on the monotreme heart supports Walmsley's opinion that the auriculo-ventricular node lies outside the sinus region of the right auricle. Moreover, Shaner (11) finds that the auriculo-ventricular node first appears in the 9 mm. calf embryo behind the posterior endocardial cushion, at which time the auriculo-ventricular ring is a complete and unbroken muscular ring around the auriculo-ventricular canal, continuous above with the auricular muscle and below with the ventricular muscle.

The auriculo-ventricular bundle and its divisions
(Plate II, fig. 8; Plate III, figs. 12 and 13)

From the ventrocaudal part of the auriculo-ventricular node the auriculo-ventricular bundle passes forwards, at first through the connective tissue on the right side of the cartilago cordis in *Platypus*, or through the trigonum fibrosum in *Echidna*, thence continuing embedded in connective tissue on the upper border of the muscular ventricular septum. Here it lies nearer the right than the left side of the septum, being close to the endocardium on the right side, but separated from the endocardium on the left side of the septum by a thick layer of connective tissue. At the anterior part of the upper border of the muscular septum the bundle divides into right and left limbs, the bifurcation of the bundle sitting saddle-wise on the upper border of the muscular part of the ventricular septum (Plate III, fig. 13). The auriculo-ventricular bundle is a relatively massive structure in both *Platypus* and *Echidna*, and consists of a compact rounded bundle of parallel Purkinje fibres (Plate III, fig. 11). These fibres are large, having an average diameter of about 20 μ, and contain two, or occasionally three, round, central nuclei. Around the nuclei there is a clear cytoplasmic zone, longitudinal myofibrillae being limited to the periphery of the cell. Transverse striation is easily recognisable in these fibrillae, but is not so marked as in the myocardial fibres proper. Although the auriculo-ventricular bundle is surrounded by connective tissue, some of the specialised fibres appear to establish continuity with the myocardial fibres of the upper part of the ventricular septum, and the lower part of the bundle presents a streaky appearance (in the stained sections, Plate III, fig. 12) owing to the fact that some of the more deeply staining septal myocardial fibres are interspersed among the specialised fibres of the bundle. A few nerve fibres can be identified among the special bundle fibres and can be traced into continuity with those in the auriculo-ventricular node.

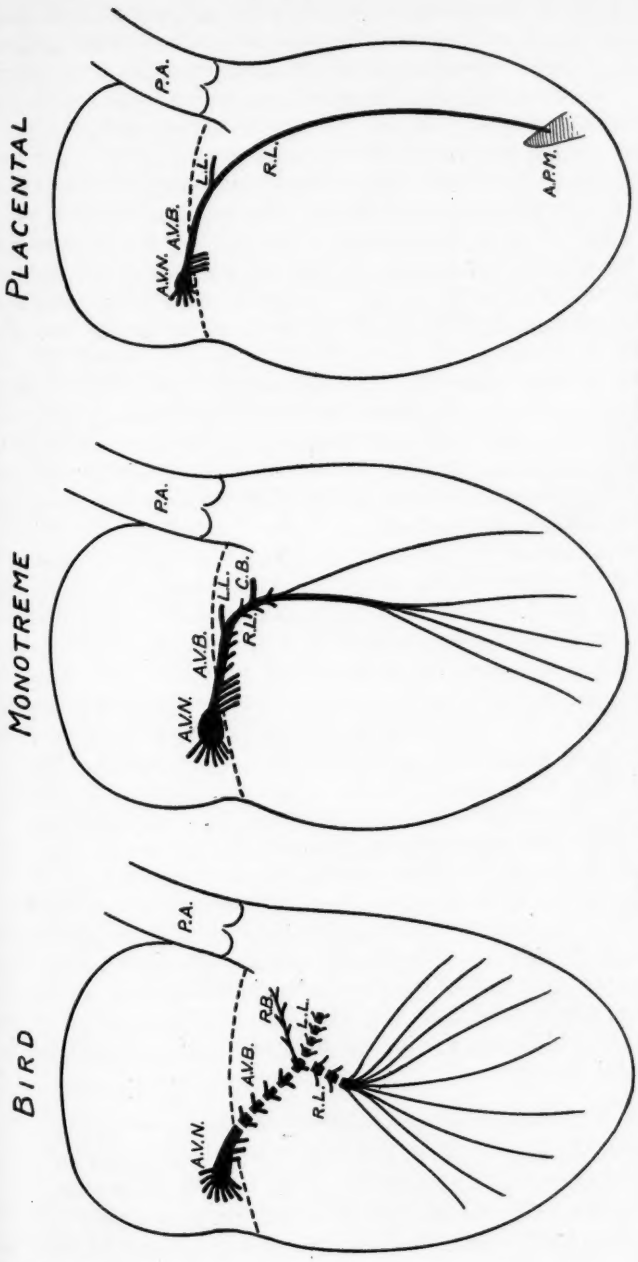
The right limb of the auriculo-ventricular bundle

From the bifurcation of the auriculo-ventricular bundle the right limb runs caudally beneath the endocardium on the right side of the ventricular septum, immediately behind the conus arteriosus. At first it has the form of a round bundle (Plate III, fig. 14), but about one-quarter of the way down the right side of the ventricular septum it broadens out and divides into an anterior and a posterior branch (Plate IV, fig. 15). The specialised fibres of the right limb of the auriculo-ventricular bundle have the same characters as those of the main bundle. The right limb has a delicate connective tissue investment, but some of the deeper specialised fibres come into apposition with the neighbouring septal myocardial fibres, and indeed appear to establish continuity with them. Also, just beyond the commencement of the right limb, many of its specialised fibres become continuous with the myocardial fibres of the conus arteriosus. The anterior, smaller, branch of the right limb of the auriculo-

ventricular bundle (Plate IV, fig. 16) runs caudally and ventrally, as a single rounded bundle, beneath the endocardium on the right side of the ventricular septum. About two-thirds of the distance down the septum it passes beneath the endocardium of a large muscle bundle (the septo-marginal bundle) which conveys it from the septum to the free wall of the right ventricle, which it reaches a short distance above the apex (Plate IV, fig. 17). Here it passes into continuity with the sub-endocardial Purkinje network of the free wall of the right ventricle. The posterior, larger, branch of the right limb of the auriculo-ventricular bundle (Plate IV, fig. 18) runs downwards beneath the endocardium on the right side of the ventricular septum, becoming markedly flattened out, and, more than halfway down the septum, divides into four subsidiary branches (Plate IV, fig. 19). These branches, after a short course downwards beneath the septal endocardium, are conveyed from the septum to the free wall of the right ventricle in "false tendons" to become continuous with the sub-endocardial Purkinje network of the free wall of the right ventricle (Plate IV, fig. 20). On their way down beneath the endocardium on the right side of the ventricular septum, all the branches of the right limb of the auriculo-ventricular bundle are embedded in connective tissue, but in many places the deeper specialised fibres appear to establish continuity with the immediately subjacent septal myocardial fibres.

It is interesting to compare the septal disposition of the right limb of the auriculo-ventricular bundle in the monotreme heart with that in the avian heart on the one hand and with that in the heart of the placental mammal on the other (text-figure 1).

The present writer drew attention in previous communications (4, 5) to the fact that the right limb of the auriculo-ventricular bundle in the bird's heart passes from the bifurcation of the bundle (which is situated in the *depth* of the ventricular septum, about one-quarter of the distance down) to the endocardium on the right side of the ventricular septum, and there divides into several strands of Purkinje fibres which pass to the free wall of the right ventricle. The right limb of the auriculo-ventricular bundle in the heart of the placental mammal is generally described as a single, *unbranched* bundle, enveloped in a well-defined connective tissue sheath, passing down on the right side of the ventricular septum (immediately behind the conus arteriosus) and thence to the base of the anterior papillary muscle by means of the "moderator band" (septo-marginal bundle). The right limb of the bundle in the placental mammal is thus considered not to give off any branches until it reaches the base of the papillary muscle, where it passes into continuity with the sub-endocardial Purkinje network of the right ventricle. The present study shows that the right limb of the auriculo-ventricular bundle in the monotreme heart, which reaches the free wall of the right ventricle in the form of five branches, is intermediate in its arrangement on the right side of the ventricular septum between that of the much-branched right limb of the avian bundle and that of the (as usually described) single unbranched right limb of the bundle in



Text-fig. 1. Diagram to illustrate comparison of auriculo-ventricular node and bundle and right limb of bundle in avian, monotreme and placental heart. (For explanation see text.)

the heart of the placental mammal. It may be observed that the anterior branch of the right limb of the auriculo-ventricular bundle in the monotreme heart pursues a course on the right side of the ventricular septum similar to that of the entire right limb of the bundle in the heart of the placental mammal, namely, immediately behind the conus arteriosus and thence to the free wall of the right ventricle by means of the septo-marginal bundle.

The description of the unbranched course of the right limb of the auriculo-ventricular bundle in the heart of the placental mammal, from its point of commencement to its arrival at the base of the papillary muscle, is supported by Indian ink injections of the sheath of the auriculo-ventricular bundle and its divisions in the ox heart (King (21), Aagaard and Hall (22)), and by the detailed reconstructions of the system in the heart of the calf and of man (de Witt (23)).

Lewis (24), however, noted that an experimental lesion of the right limb of the auriculo-ventricular bundle in the dog's heart produced a more pronounced effect upon the subsequent electrocardiographic tracing the higher up the limb the lesion was situated. He therefore concluded that there must be early outgoing branches from the right limb of the bundle, though such have not been demonstrated anatomically.

Curran (20) in one of his figures (Plate II, fig. 10), though no special importance is attributed to it in the general text, shows a dissection of a branch given off from the right limb of the auriculo-ventricular bundle in the calf heart. This branch is given off just before the right limb enters the "moderator band," and it passes upwards and to the left into the musculature of the conus arteriosus. Ungar (25) has noted that when a well-developed septal papillary muscle is present in the right ventricle of the human heart, the right limb of the auriculo-ventricular bundle occasionally gives a branch to it. The branch of the right limb of the bundle to the conus musculature in the calf heart figured by Curran recalls the continuity of some of the specialised fibres of the right limb of the monotreme bundle with the adjacent myocardium of the conus. It also has its parallel in the recurrent branch of the auriculo-ventricular bundle in the heart of the bird, which passes upwards and to the left from the bifurcation of the bundle into the depth of the conus musculature (Davies (4, 5)). The results of Lewis's experiments and the present observations of the branching of the right limb of the monotreme bundle and the continuity of the specialised fibres of the right limb with the septal myocardium certainly warrant a careful histological re-investigation of the right limb in the heart of the placental mammal.

The left limb of the auriculo-ventricular bundle

From the bifurcation of the main bundle the left limb passes downwards immediately beneath the endocardium on the left side of the ventricular septum. It first reaches the left side of the septum immediately below the right cusp of the aortic valve, and takes the form of a broad flattened band

of specialised fibres which have the same histological characters as those of the main auriculo-ventricular bundle. It is larger than the right limb and its fibres are more loosely arranged with much connective tissue lying between groups of the specialised fibres. Some of the deeper fibres of the left limb come into apposition with the subjacent septal myocardial fibres and appear to establish continuity with them. About one-quarter of the distance down the left side of the ventricular septum the left limb divides into four branches (two main central and two small marginal) which radiate from each other as they pass downwards beneath the endocardium on the left side of the septum. These branches subdivide and eventually reach the free wall of the left ventricle to become continuous with the sub-endocardial Purkinje network on the free wall of the left ventricle either by means of "false tendons" or at the junction of the septum and free wall. The disposition of the left limb of the monotreme bundle is very similar to that of the left limb of the bundle in the heart of the placental mammal.

A marked feature of the Purkinje system in the heart of the bird is the penetration of the sub-endocardial Purkinje fibres of the auricles and ventricles into the myocardium, especially in relation to the branches of the coronary arteries (4). No myocardial penetration of the sub-endocardial Purkinje fibres of the right or left ventricle in the monotreme heart was observed in the present study; the sub-endocardial Purkinje fibres of both ventricles become continuous immediately with the adjacent myocardial fibres.

SUMMARY

1. The conducting system, of specialised structure, of the monotreme heart (*Platypus* and *Echidna*) is described.

2. The limitation of sinu-auricular nodal tissue to the region of the right sinus valve in the presence of the intersepto-valvular space of the right auricle is evidence that the disappearance of the intersepto-valvular space in the higher mammalian heart is not the prime factor in the "condensation" of the sinu-auricular ring of the lower vertebrate (piscine and reptilian) heart.

3. The position of the sinu-auricular and auriculo-ventricular nodes in relation to the sinus valves is discussed.

4. The branched arrangement of the right limb of the auriculo-ventricular bundle in the monotreme heart is described and compared with that of the right limb of the bundle in the bird's heart previously described by the present writer, and with the present conception of the right limb of the bundle in the heart of the placental mammal.

I wish to express my gratitude to my former chiefs, Prof. G. Elliot Smith and Prof. J. P. Hill, and to my present chief, Prof. D. M. Blair, for their interest and advice, also to Mr F. Pittock and Mr E. O. Lloyd, technical assistants at University College, for the preparation of the material to illustrate the present work.

DESCRIPTION OF PLATES I–IV

PLATE I

Fig. 1. Transverse section through lower part of right auricle of *Platypus* heart. Low power.
Fig. 2. Transverse section of upper part of free wall of right auricle. *Platypus*. Low power.
Fig. 3. High power view of part of fig. 2.
Fig. 4. Transverse section of upper part of free wall of right auricle. *Echidna*. Low power.

PLATE II

Fig. 5. Transverse section of upper part of free wall of right auricle. *Platypus*. Low power.
Fig. 6. Transverse section through appendix of left auricle. *Echidna*. High power.
Fig. 7. Transverse section of left auricular appendix. *Echidna*. High power.
Fig. 8. Transverse section through upper border of ventricular septum. *Platypus*. Low power.
Fig. 9. Transverse section through lower border of auricular septum. *Platypus*. High power.
Fig. 10. Figure of Curran's dissection of auriculo-ventricular node and bundle in heart of calf.

PLATE III

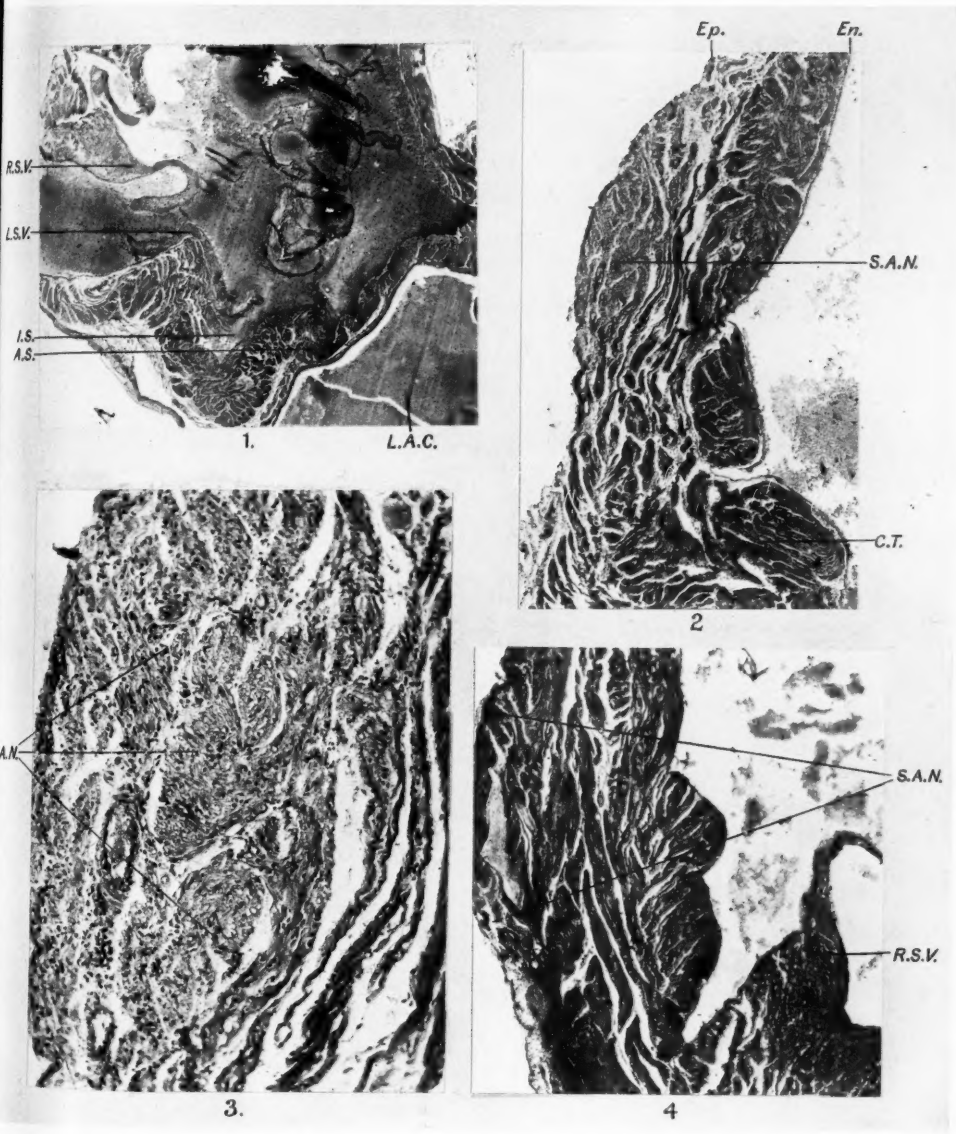
Fig. 11. High power view of transverse section through auriculo-ventricular bundle. *Platypus*.
Fig. 12. Transverse section through upper border of ventricular septum. *Platypus*. Low power.
Fig. 13. Transverse section through upper border of ventricular septum a little below fig. 12. *Platypus*. Low power.
Fig. 14. Transverse section through upper part of ventricular septum. *Platypus*. Low power.

PLATE IV

Fig. 15. Transverse section of ventricular septum about one-quarter of the distance down the septum. *Platypus*. Low power.
Fig. 16. Transverse section through ventricular septum below fig. 15. *Platypus*. Low power.
Fig. 17. Transverse section through ventricular septum about two-thirds of the distance down the septum. *Platypus*. Low power.
Fig. 18. Transverse section through ventricular septum about halfway down the septum. *Platypus*. Low power.
Fig. 19. Transverse section through ventricular septum below fig. 18. *Platypus*. Low power.
Fig. 20. Transverse section through ventricular septum a short distance above the apex. *Platypus*. Low power.

ABBREVIATIONS USED IN PLATES AND TEXT-FIGURE

A.S.	Auricular septum.
A.V.B.	Auriculo-ventricular bundle.
A.V.N.	Auriculo-ventricular node.
B.	Bifurcation of A.-V. bundle.
C.B.	Branch of right limb of A.-V. bundle to conus arteriosus.
C.C.	Cartilago cordis.
En.	Endocardium.
Ep.	Epicardium.
F.T.	False tendons.
I.S.	Intersepto-valvular space.
L.A.C.	Left auricle cavity.
L.L.	Left limb of A.-V. bundle.
L.S.V.	Left sinus valve.
L.V.C.	Left ventricle cavity.
N.C.	Nerve cells.
N.P.	Nodal prolongation.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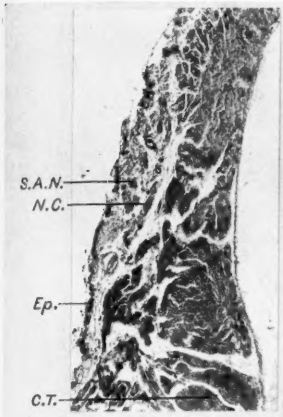

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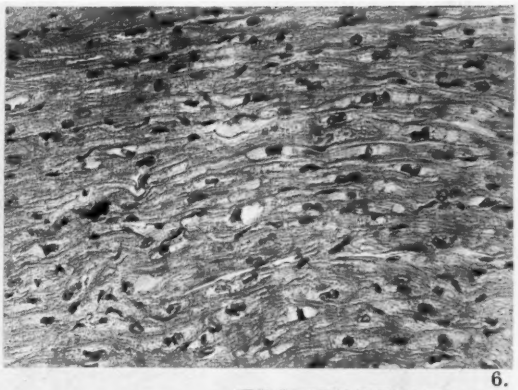

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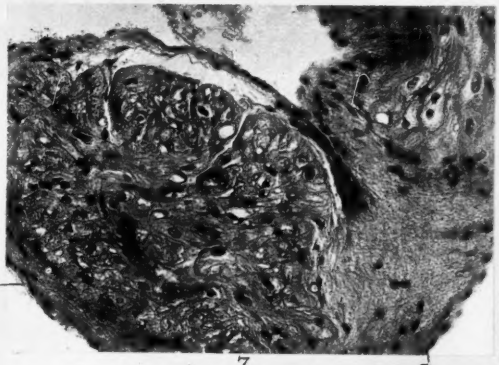

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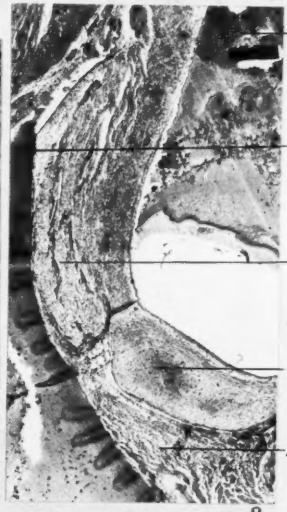

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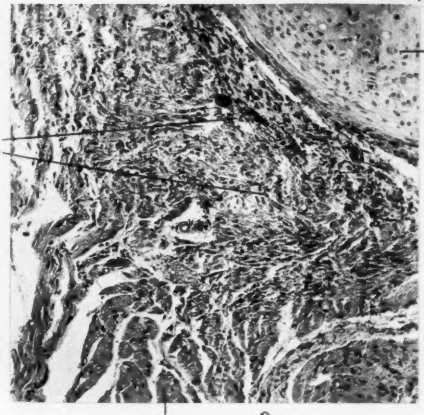

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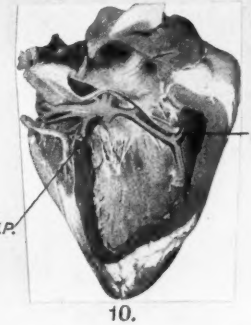

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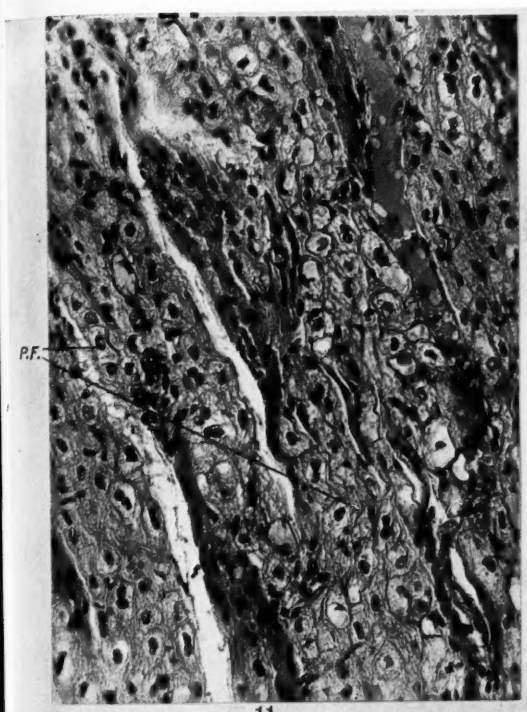

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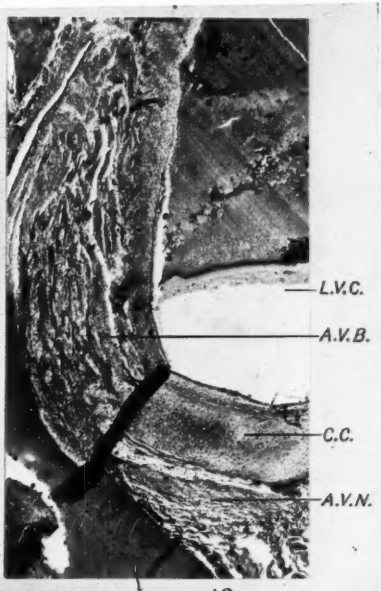

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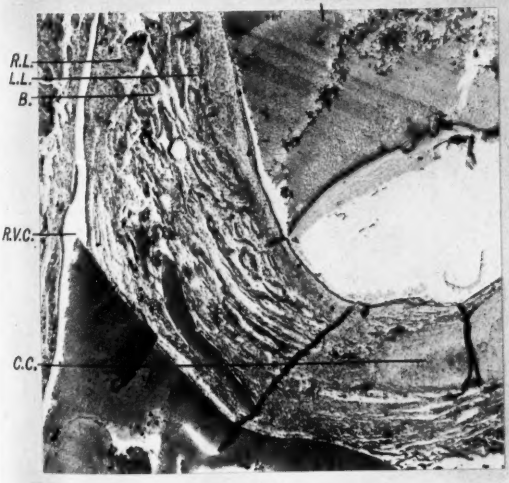

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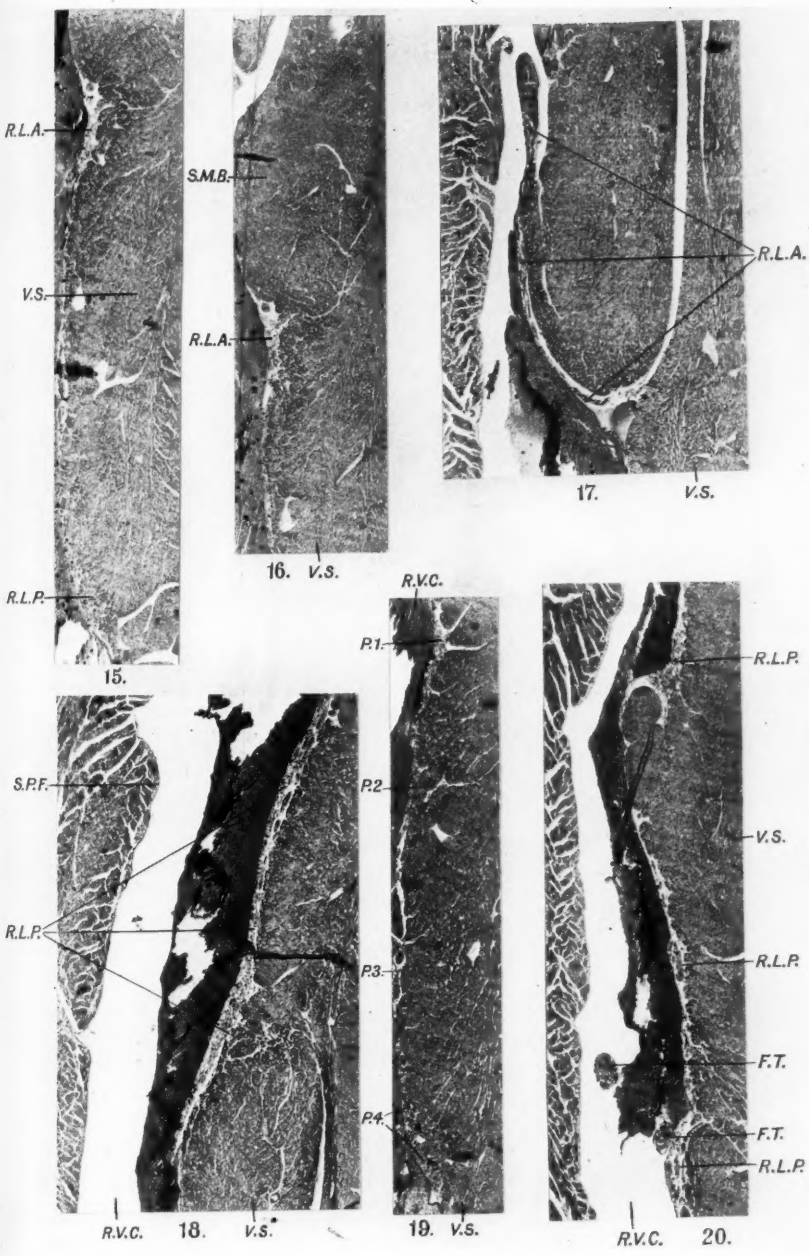
R.L.A.
V.S.
R.L.P.
15.
S.M.B.
R.L.A.
16. V.S.
R.L.A.
17. V.S.
R.V.C.
P.1.
P.2
P.3.
P.4.
19. V.S.
R.L.P.
V.S.
R.L.P.
F.T.
F.T.
R.L.P.
R.V.C. 20.
S.P.F.
R.L.P.
R.V.C. 18. V.S.

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P.F. Purkinje fibres.
R.A.C. Right auricle cavity.
R.L. Right limb of A.-V. bundle.
R.L.A. Anterior branch of right limb of A.-V. bundle.
R.L.P. Posterior branch of right limb of A.-V. bundle.
(P 1, P 2, P 3, P 4. Subdivisions of *R.L.P.*)
R.S.V. Right sinus valve.
R.V.C. Right ventricle cavity.
S.A.N. Sinu-auricular node.
S.M.B. Septomarginal bundle.
S.P.F. Sub-endocardial Purkinje fibres.
V.S. Ventricular septum.

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TWO DETAILS ABOUT THE NECK OF THE FEMUR: (1) THE EMINENTIA. (2) THE EMPREINTE

By P. N. B. ODGERS
Department of Human Anatomy, University of Oxford

I THINK all previous accounts of these two points in the neck of the femur have been based mainly on the examination of dried bones. For my purpose I collected the head and neck of pairs of femurs, right and left, from 52 individuals of known age and sex—104 bones in all—and examined them in the moist state. The bones may be grouped as follows:

Ages	No. of male femurs	No. of female femurs
20–29	0	4
30–39	8	6
40–49	8	4
50–59	8	4
60–69	20	16
Over 70	20	6
Total	64	40

Further, to compare my figures with a mixed lot of dried femurs, I examined the whole skeletons in the Museum of the Royal College of Surgeons. Here, as will be remembered, are a collection of African, Australasian, and Asiatic skeletons, together with those of J. Wilde and C. Byrne. I only took those to which a definite age, which I presume is approximately correct, is given. From them, too, I obtained a much younger series of bones than my own, which were largely derived from the dissecting room. The male femurs number twenty-eight, and all of these, save four, are between 20 and 40 years of age: similarly, the female bones, sixteen in all, are all between the ages of 16–39, with the exception of one pair. In Tables I and III these femurs appear as "R.C.S.," but are not included in any analyses of these tables in the text.

THE EMINENTIA

The eminentia articularis colli femoris was figured by Henle and Cruveilhier without any description of it in their texts. It was given this name by Fick, and first accurately described by Sudeck.

If well marked (figs. 1, 4, 7, 9, 10) it stands out uncovered by retinacula—and it is the only part of the femoral neck, which is uncovered by them—as a prominent compact bar stretching from the superior tubercle of the intertrochanteric line to the head of the bone. If it is not an obvious projection, its presence can still be recognised by a finger and thumb passed round the neck.

It is almost constantly present: my 104 femurs show it more or less in 100, i.e. 96 per cent.: in male bones I find it in 100 per cent., in female bones in 90 per cent. It is found to vary in the degree of its development with the sex and with the age of the bone and with the side to which the bone belongs, while, if it is well marked, its medial extremity will be covered to a variable amount by an extension of the cartilage of the head. It may be said to be developed *pari passu* with the intertrochanteric line and is best seen in well-marked massive male bones.

Table I shows the femurs divided into three age groups and the degree of development of the eminence noted in each group. When I first began this investigation I was dealing exclusively with material of 60 years of age or over, and I thought that there was an absolute sexual difference in the development

Table I

Age	No. of femurs	Marked eminentia	Slight eminentia	Absent	Marked eminentia (%)
		Adult males			
39 and below	8	7	1	0	87·5
40–59	16	15	1	0	93·7
60 and over	40	36	4	0	90
		Adult females			
39 and below	10	3	7	0	30
40–59	8	3	3	2	37·5
60 and over	22	2	18	2	9
R.C.S.		Adult males			
39 and below	20	14	6	0	70
40–59	6	6	0	0	100
60 and over	2	0	2	0	—
		Adult females			
39 and below	14	4	5	5	28·5
40–59	2	1	1	0	—

of this eminence. This was proved not to be absolute, when adult bones of all ages were considered, but the difference between male and female bones is still sufficiently striking. Taking my own series, 90·6 per cent. of male bones present a marked eminence compared with 20 per cent. of female bones. Figs. 1, 7 and 9 show well-marked eminences in male bones. In contrast to these compare fig. 2, which is from a female, aged 52, and which shows practically no evidence of it. Fig. 3, on the other hand, shows a male femur (aged 55) with a very poorly marked eminence, while fig. 4 is from a young woman, aged 28, and shows a good eminence with considerable prolongation of the articular cartilage.

Comparing right and left femurs from the same individual, I note that of sixty-four male femurs, the eminence is better developed on the left one in eleven instances (17 per cent.), on the right in three (4·6 per cent.). In female bones, however, the preferences are equally divided: in the forty female femurs the eminence is better marked on the right bone in four and on the left in four. At the same time, if one takes only female femurs with well-marked

eminences under 60, of the six instances of this, four occur on the left to two on the right bones.

Sudeck showed that the eminentia corresponds to the last part of the femoral neck to ossify—"originally a common epiphysial line for the head and great trochanter is split by the ossifying neck into two, but the separation does not occur above and in front and at this point continuity of the whole epiphysial line remains for some years." I have been able to confirm Sudeck's observations on such young dried bones as I have been able to examine here and at the College of Surgeons. At 3, and still at 7 years of age, the great trochanter and the head of the bone are connected by a strip of cartilage: at 12, this has ossified at the centre, cartilage remaining laterally, which will ossify later with the epiphysis of the great trochanter as the superior tubercle, while the medial end of the strip is represented by a slight projection of the cartilage of the head of the bone. At 18 or 19 years of age both male and female bones have a well-marked eminence. It would appear from a consideration of Table I that, while this persists and will become, if anything, more pronounced with age in males, in females there is the opposite tendency. In a female bone, aged 22, in this department there is practically no eminence, while C. Byrne's femurs, of the same age, in the Hunterian Collection show them well developed. This disparity is seen to be most marked in femurs from the aged: in those of 60 years old or over, a marked eminence occurs in 90 per cent. of male to 9 per cent. of female bones.

As Poirier pointed out, one commonly sees both above and below the junction of the eminence with the head of the bone that the cartilage of the head presents a margin concave lateralwards. At the medial end of the eminence these two concavities meet and form a more or less pointed projection, which varies very much in different bones, but which, as a rule, is insignificant. On the other hand, it may extend on to the eminence for as much as 1·5 cm. To be accurate one should speak of fibro-cartilage as making this extension. In every diarthrodial joint the junction of the synovial membrane and the articular cartilage is marked by a ring of fibro-cartilage (Testut). I had horizontal sections made through the eminence and the adjacent part of the head of the bone in the femurs photographed in figs. 6 and 7. These both show that, close to the head the eminence is covered superficially by fibro-cartilage, while the deeper layers are still hyaline. As one traces the section lateralwards, while the fibro-cartilage thickens and becomes more fibrous and is continued ultimately as the periosteum, the deeper hyaline cartilage becomes less and less conspicuous and entirely disappears at a variable distance from the head. This extension occurs most frequently when the eminence is well marked (figs. 4, 9). While exact figures may be rendered slightly inaccurate owing to the erosion of the cartilage in this situation, I find (Table III) such a marked cartilaginous extension present in twenty-three of my sixty-four male femurs (35·9 per cent.), while forty female femurs show it only four times (10 per cent.). If one divides the male bones into two age categories, below 60 and 60 and

above, the percentages are practically the same—29 per cent. for the first group, 30 per cent. for the second. Divide the female bones similarly and all the instances occur in subjects below 60 (22 per cent.); above this age no such extension is found in any case in female bones. It appears, then, to be correlated with a well-developed eminentia, and is most marked when the medial end of this is pronounced enough to be flush with the head. In no case, except in one pair of femurs from a woman, aged 52, is there any marked extension of the head cartilage in the absence of a well-marked eminence.

THE EMPREINTE

This was first described by Allen in 1882 as the "Cervical Fossa": it is better known as the "Empreinte Iliaque" of Poirier, who thus named it some 10 years later. In the great majority of femurs from persons over 40 there will be found on the anterior surface of its neck, just where the latter joins the head, a depressed irregular roughened area, in which the bone is eroded to a greater or lesser extent. Figs. 4, 6, 7, 8, 9 and 10 show varying degrees of this, from what I have called, for want of a better term, a depression, where there is merely a smooth marking without apparent abrasion of the surface in this situation (figs. 4, 6, 7), to a very marked erosion as in fig. 10. Figs. 6, 7 and 8 all come from persons of about 40 years of age, and are interesting as showing early stages of the empreinte. Fig. 6 is a female bone (age 40) with a slightly marked eminentia, and shows a shallow longitudinal groove. In the next figure (7) of a male bone (age 41) this groove is more pronounced and is localised on the medial end of a much better marked eminence. In both of these the grooves, although apparently smooth, show microscopically that the fibro-cartilage is already irregularly fretted. Fig. 8 (male, aged 39) gives the appearance of almost having had a bit of fibro-cartilage sawn roughly away or torn off the eminence, leaving laterally an overhanging tag. Here the bone is actually exposed. Such an empreinte—be it simply a depression or an erosion—always commences on the inner side of the eminence and, in many instances, is confined to this. In the more marked cases it extends below this, parallel to the intertrochanteric line, as far as the lower border of the front of the neck. The lateral edge of such an empreinte is often clearly defined by a bony ridge—the "bourrelet osseux" of Poirier or the "capsular ridge" of Walmsley.

As regards their frequency, putting the different varieties together, I find them in 92 per cent. of male, and in 67·5 per cent. of female bones. In Table II I have divided these empreintes into three groups—depressions, slight erosions and marked erosions. While one may see quite a considerable depression, as in fig. 7, while in another older bone (fig. 9), there is a much smaller localised erosion, if one analyses these figures, one finds that the older the individual, the deeper is the empreinte. In male bones below 60, twenty-four femurs show twelve depressions (50 per cent.) to nine erosions of varying extent (37·5 per cent.), while three bones show neither (12·5 per cent.): above 60, forty femurs exhibit eleven depressions (27·5 per cent.) to twenty-seven erosions (67·5 per

cent.), while two bones are unmarked (5 per cent.). Taking the female bones the same progression is observed. Below 60, eighteen femurs show six depressions (33·3 per cent.) to three erosions (16·6 per cent.) with nine (50 per cent.) unmarked: over 60, there are twenty-two femurs, with three depressions (13·6 per cent.), fifteen erosions (68 per cent.) with four (18 per cent.) unmarked. The youngest male bone to show any marking is 36 years old, while an erosion is first seen at 39. A female bone, aged 28, has a slight depression (fig. 4); this is much better marked in another female femur, aged 34, while an erosion first appears at 37. In the R.C.S. skeletons I found marked erosions on the femurs from a Bush woman, aged 20, and from an English woman, aged 24, while the youngest male femurs to show any marking were those of an Arawak Indian, aged 27, and of C. Byrne, aged 22. At the other end of the scale one finds two

Table II

Age	No. of Bones	De-pression	Slight erosion	Marked erosion	No marking	Frequency of empreinte (%)
			Male femurs			
39 and below	8	4	0	2	2	75
40–59	16	8	3	4	1	93·7
60 and over	40	11	9	18	2	95
			Female femurs			
39 and below	10	2	1	0	7	30
40–59	8	4	2	0	2	75
60 and over	22	3	5	10	4	81

male bones from different individuals over 60, which show no trace of an empreinte, while two pairs of bones from men, aged 73 and 83 respectively, only have the faintest depressions. Again, four female bones, 64 and 65 years of age, show neither erosion nor depression. (It is interesting to note that these four femurs are the only ones out of twenty-two female bones over 60, which exhibit no evidence of a degenerative arthritis—erosion or lipping of the cartilage of the head of the bone.)

A comparison between right and left male bones shows that, while in eight cases the right femurs have a more marked depression or erosion than the left, in eight others the opposite is the case. Taking the female bones, on the other hand, in one instance the left femur shows an erosion while the right has none, and in eight others the empreinte is better marked on the left than on the right side, compared with three instances where the reverse condition obtains.

DISCUSSION

There has arisen some confusion in the accounts of the eminentia and the empreinte in the literature owing to authors confusing the names, which were originally given to these two different things. Henke first and then Poirier both noticed the occasional extension of the head cartilage on to the neck and this was subsequently generally known as "Poirier's facet." This is not Poirier's empreinte, as originally described by him—"lorsque cette avancée cartilagineuse n'existe pas en avant, on trouve à sa place une empreinte

rugueuse, à contour plus ou moins net, circulaire ou ovalaire: c'est l'empreinte iliaque du femur." Fick showed that the cartilage extension almost always corresponds to a marked "beetartige Erhabenheit," which he called the Eminentia articularis colli femoris, but which he wrongly says Poirier had already named the empreinte iliaque. Here seems to be the origin of the confusion—an elevated ridge of bone and a depression, or actual bone erosion, being called the same thing in different languages. For instance Pearson puts Poirier's facet, the empreinte and the eminentia in the same category and describes prolongation and excavation types of facet, while he quotes Sudeck, who was dealing solely with the eminentia, as finding Poirier's facet practically always present. Again, Meyer only recognises the eminentia as a marked extension of the head cartilage—he only finds it in seven out of 163 femurs—while in another place in the same paper he appears to regard Walmsley's capsular ridge and the eminentia, as described by Sudeck, as the same thing. These instances are enough to show how difficult it is to compare the description of these two points as given by different authors and I had better again define what I mean myself by the eminentia. I have followed Sudeck in describing the eminentia as a raised ridge of bone, practically constantly present with different degrees of distinctness in all bones, stretching from the head of the femur to the superior tubercle of the intertrochanteric line. As Sudeck showed, this is the last portion of the neck to ossify and furthermore is the "äussere Betonung einer besonders starken Spongiosastelle im innern," corresponding in the whole of its extent to the summit of the arch of the spongy lamellae, which gives the neck strength against traction in a downward and backward direction and indicates a strengthening here of the tie system. The medial portion of this ridge may be covered to a varying degree with an extension of fibro-cartilage from the head of the femur and, while this extension is most marked in cases of prominent eminences, it should not be made the criterion for the presence or absence of this ridge of bone.

The significance of the eminentia

I have shown that the eminence is best seen in male bones, between 40 and 60 years of age, with well-marked intertrochanteric lines with prominent tubercles. As Walmsley pointed out (although he did not call his "lateral smooth area" the eminentia), it is comparable to the pulley on the lesser sacro-sciatic notch, over which the tendon of the obturator internus plays at its exit from the pelvis: over the eminence the anterior part of the capsule stretches in extension of the thigh. The marked sexual difference in the development of this ridge, as is seen in Table I, is, I think, significant. The characteristic female gait, whatever its cause, whether it be correlated with a shorter ilio-femoral ligament or no, is essentially associated with less extension at the hip joint, and it is fair to assume that there is never the same pressure on the front of the neck of the femur in the female as in the male. The absence of eminentia strikes one most forcibly, when one compares an anthropoid bone with a human male femur.

In such anthropoid femora as I have been able to examine, in two orangs there is just the faintest evidence of an eminentia ridge to the finger: otherwise in gorilla, chimpanzee and gibbon femurs the neck presents a perfectly even surface at its junction with the head, which overhangs it as a mushroom does its stalk. With this is associated complete absence of a tuberculated intertrochanteric line. The usual shambling anthropoid gait can rarely necessitate any full extension at the hip. Again, the slightly better development of this ridge on the left as compared with the right femur (17 per cent. to 4·6 per cent.) can well be correlated with the left lower extremity being the "better leg."

If one allows, then, that the eminentia acts as a pulley bar to take the pressure of the joint capsule, one would look on the extension of the head cartilage on to its medial portion as a second line of defence. While I have not a sufficient number of bones from young adults in my present series as evidence on this point, and although one femur from a female of 28 (fig. 4) shows a good extension, I have not seen signs of such cartilaginous extensions on any dried bones, that still show marked external traces of epiphysial lines, while the younger R.C.S. bones show this less frequently than do my own collection of older ones. I would, therefore, agree with Walmsley, who says that "they have never presented themselves in the young subject and always in my series they have been associated with strong bony ligamentous markings and with powerful capsular bands." In contact with such a cartilaginous extension will be the circular fibres forming the zona orbicularis (*vide infra*), and these, as Fick says, in extension of the leg in the upright position are screwed up by the spiral twist of the ilio-femoral ligament against the acetabular margin and surround the junction of head and neck like a valve. This is the part of the eminence, then, that has to take the greatest strain, and in this connection the femur photographed in fig. 11 is of interest. It came from a woman, aged 59, with a very extensive chronic arthritis of either hip joint, and is not included in the series of bones I am considering. It shows, as does its fellow, a marked overflow of hyaline cartilage on to the neck in this situation and nowhere else, as if an attempt were being made to form a good eminentia.

The empreinte

In Table III I have put together for comparison my own figures of the frequency of the occurrence of this with those of Pearson, Parsons and Meyer. The same table shows also the percentage frequency of the occurrence of an extension of cartilage on to the neck. Some of the differences between these percentages can be explained by the fact that my material was fresh and theirs was dry. I can well believe that many of the depressions I find would not show on the dry bone: again, the ages of the bones they examined were unknown. The following similarities may, however, be noted:

(1) The empreinte is seen more frequently in male than in female bones.

(2) While in males the figures for either side are practically the same, in females it is found more often on the left side.

(3) An extension of the cartilage from the head of the bone occurs much more frequently in male than in female femurs.

I cannot follow Pearson in his division of the empreinte into prolongation and excavation facets or in his further subdivision of the latter. Meyer joins Poirier and Bertaux in maintaining that "whenever marked excursions of the articular surface of the head upon the neck are present in this area, the imprint is absent." Meyer, however, himself figures "rare transition forms" and Pearson has numerous combinations of imprint with prolongation facet—"one, two or even three phases of our facet may occur on the same bone." I have never seen in this series any instance of a marked cartilaginous extension that does not show either a depression or an actual erosion. Thus in twenty-three instances of this in male bones, twelve had marked erosions, while eleven had depressions: in the female bones there were four instances, of which two were eroded and two had slight depressions. As is well seen in figs. 7, 8 and 9, it is just in this situation that the eminentia is first depressed and then eroded. From here, with increasing wear and tear, the fossa may extend laterally, but be still confined to the eminence or, more frequently, will ultimately involve the surface of the neck below this, as in fig. 10.

Table III

	Empreinte				Extension of cartilage	
	Male		Female		Male	Female
	R. (%)	L. (%)	R. (%)	L. (%)	(%)	(%)
My own series	92	92	65	70	35·9	10
Pearson — London femora	87·3	88·3	78·1	81·4	35·9	12
Pearson — Naquada femora	80·85		68·32		15·83	11·78
Parsons	79	79	58	67	—	—
R.C.S.	60·7		43		21·4	12·5
Meyer (sex of femora unknown)	R. 71·6		L. 60·9			

The cause of the empreinte

Various reasons for the appearance of the empreinte have been given by different observers and these may perhaps be conveniently divided into two categories.

I. Poirier, Evangeli Tramond and Regnault showed that in exaggerated flexion of the thigh on the pelvis the upper and inner part of the neck of the femur rubs against a slight projection of the acetabular margin just beneath the anterior inferior iliac spine. This led Charles to regard Poirier's facet as one of the squatting facets. Fick, Parsons and Walmsley have shown, however, that medial rotation with extreme flexion are necessary to get facet and acetabular

border into contact. My dissections certainly confirm this, and it is obviously a most unnatural position for any person to adopt. More recently Pearson and Meyer have both suggested that such contact occurs during sleep. The former writes: "Were it needful—which we doubt—to find an habitual posture likely to produce by pressure Poirier's facet, we would suggest the lying full length on the side in bed with the upper lower limb thrown forward, as the most likely position to induce considerable pressure on the observed region of the facet in the under lower limb." Meyer maintains that, during sleep, apart from the use of the upper extremity, contact of the femoral neck with the ligamentous acetabular lip is the only thing that prevents forward rotation of the trunk upon the extremity in contact with the underlying surface: the range of the flexion of the thighs in the resting posture, peculiar to the individual, will determine the length of the iliac imprint, while the preference for lying on one side or the other during sleep would account for differences observed on two sides of the same body or in different bodies. The obvious objection to such a theory is that one has to imagine that the fibro-cartilaginous acetabular rim is capable of making such a marked erosion as in fig. 10 during rest. The one essential factor in the production of any secondary groove or ridge on a bone must, surely, be movement[1].

II. In the second category I would include observations, which put the cause of the empreinte down to friction with the anterior part of the capsule of the hip joint or with things in immediate contact with this.

(*a*) It has been suggested that the iliopsoas tendon, especially in full extension, is in relation here with the femoral neck. I would certainly agree with Walmsley that the tendon is medial to the empreinte and, when the bursa beneath the tendon communicates with the joint, it is the lateral part of the head of the bone which is exposed. The muscular iliacus rather lies over the empreinte, taking some origin from the front of the capsule here, and can hardly be suggested as a causative factor.

(*b*) Walmsley maintains that the vertical limb of the ilio-femoral ligament, in the position of complete extension, is responsible for this erosion. Meyer's criticism of this explanation is threefold. In the first place, he says that he cannot recall any other instance in the body of intermittent moving pressure from a tendon or ligament producing a roughening of the underlying bony surface. To this I would reply by asking if the neck of the femur is not unique in the friction it sustains from the joint capsule in full extension of the thigh in comparison with its bony make-up. The only other instance that occurs to one, where comparable moving pressure exists, is against that portion of the head of the astragalus in contact with the spring ligament. Here I have noticed occasionally that, while the rest of the articular surface is smooth and intact, the cartilage is eroded or even the cancellous bone is exposed. Secondly, he

[1] Walmsley describes certain markings at the margin of the head of the femur, which he suggests are due to contact with the acetabular margin in complete extension, but which he differentiates quite definitely from the empreinte I am considering here.

asks why the lateral part of the eminence is smooth, while only the inner part is eroded, if capsular pressure is responsible for both. Lastly, he points out that the main direction of the empreinte usually makes an angle with this limb of Bigelow's ligament. With this last criticism I would certainly agree.

(*c*) In 1915, Parsons showed that the ridge on the front of the neck of the femur (which corresponds, I take it, to Walmsley's capsular ridge) was the outer limit of a groove transmitting a special band of zonular fibres, which gripped the head of the femur lateral to the articular area. These circular deepest fibres of the capsule—the zona orbicularis—lying directly beneath the synovial layer, although described accurately by Fick and Welcker years ago, have not yet been recognised adequately in the usual accounts of the hip joint. Making a complete circle, they are almost as well marked in the front as at the back of the joint and are firmly attached to, and difficult to separate from, the more superficial longitudinal ligaments, the distortions of which they must accurately follow. At the upper border of the neck they form a stout narrow band, which tends to broaden out somewhat as it is traced anteriorly and is least distinct below. In every dissection, in which I looked for it, the most medial part of this zona, appearing in many cases as a discrete band, lay in a cervical erosion or depressed the inner end of the eminence. In fig. 6 the marking made by these circular fibres is well seen, while fig. 5 shows a flap of capsule (*C*) turned back from the front of the joint, and the cut zona orbicularis (*Z*) lying in a sharply defined empreinte (*E*). *B* in this figure indicates the cut vertical limb of the ilio-femoral ligament.

I would then regard the extension of the cartilage of the head of the femur and its erosion as being due to the same agent. I have suggested above that the eminentia acts like a pulley bar for the anterior part of the capsule, and that pressure and friction must be felt most by its medial part in contact with the circular fibres, which are screwed against it during full extension of the thigh. It is here that we get the fibro-cartilage extension as a protection against this friction, and it is here that we see the first evidence of depression or erosion—the breakdown of that protection. This difference, both in the anatomy of the capsule and in the pressure it must bring to bear on different parts of the bone, is the answer to Meyer's objection that capsular friction cannot make one part smooth and another part rough. It has been pointed out already that there must be a considerable difference between the degree of capsular pressure sustained by male and female bones: the marked sexual difference in the incidence of the empreinte, which all observers have noted (Table III), would be in consonance with this. The exact shape and the exact situation of an erosion, which latter led Pearson to divide them into three categories, will depend on two factors, on the breadth of the zona orbicularis anteriorly or better, perhaps, on how discrete a bundle the most medial part of it forms, and on the degree of the development of the eminentia. Obviously the more pronounced the eminentia, the more will it take the capsular pressure off the neck below it and the longer localised to it will be the resulting erosion.

I must thank Prof. Thomson for much valuable advice, Prof. Sir Arthur Keith for permitting me to examine the skeletons in the Museum of the Royal College of Surgeons and Mr W. Chesterman for the production of these photographs.

SUMMARY

1. The material studied consists of fifty-two pairs of femurs of known age and sex, which were examined in the fresh state.

2. The eminentia articularis colli femoris is a ridge of bone, which runs from the superior tubercle of the intertrochanteric line to the head of the femur: it is much better marked in male than in female bones and is not seen in the anthropoids. In over a third of male femurs its medial portion is covered by fibro-cartilage, which extends on to it from the articular margin. The eminence acts as a pulley bar for the anterior portion of the capsule in extension of the hip joint.

3. The empreinte of Poirier or the cervical fossa of Allen commences as a depression on the medial end of this eminentia: as this deepens, the fibro-cartilage is destroyed and the bone is eroded. It is more often seen in male than in female bones, and, with some exceptions, the older the individual, the deeper will be the empreinte.

4. The circular fibres of the hip-joint capsule—the zona orbicularis—are well marked anteriorly. These are in contact with the medial end of the eminence and are responsible for the appearance of a depression or an erosion in this situation.

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Fig 6. F,40

Fig 7. M,41

Fig 8. M,39

Fig 9. M,45

Fig 10. M,79

Fig 11. F,59

THE CRANIOPHARYNGEAL CANAL IN MAN AND ANTHROPOIDS

By A. J. E. CAVE, M.B.

Senior Demonstrator in Anatomy, University of Leeds

So infrequent is the occurrence of the genuine *canalis craniopharyngeus medius* in the adult human cranium (0·2 per cent. skulls), that any particular instance of such appears worthy of record, particularly when, as in the present case, concomitant departures from the normal are manifest elsewhere in the same subject. It is here not so much intended to review the literature of the craniopharyngeal canal, as to describe briefly a given example in man, and to augment our knowledge of its incidence in the anthropoid series.

CRANIOPHARYNGEAL CANAL IN MAN

(*a*) *Case report*

The present specimen[1] was discovered in a 38-year-old male recently dissected in this department, the cervical spine and skull being collected during routine maceration; there is no clinical history, nor are the bones of the extremities available. The cranium discloses a somewhat asymmetrical sphenoid, presenting considerable backward extension of its anterior clinoid processes, with ossification between each of these and a well developed middle process to form the carotico-clinoid foramen (fig. 1); the dorsum sellae is well formed, but its uppermost portion—the transverse bar bearing at its extremities the posterior clinoid processes—is independent of the rest of the bone to which it has attachment by fibrous tissue only (fig. 2). A deep pituitary fossa, well ringed in by bone, presents in its floor (as does the pre-sphenoid) numerous minute vascular foramina, as well as a wide circular hole (3·5 mm. diameter), the mouth of a craniopharyngeal canal which the probe discovers to extend for a distance of 16 mm. downwards and forwards through the median septum of the sphenoidal sinus to a vomerine termination in the nasal septum; the undeviating median course of this canal (presumably occupied by pituitary tissue *in vivo*) is clearly demonstrable by skiagram upon the insertion therein of a metal probe (see fig. 3). There is ossification of the pterygospinous ligaments, and of the uppermost inch or so of the stylohyoid ligaments; numerous bony spicules project from the external pterygoid plate, the rim of the foramen magnum and from the nuchal portion of the occipital.

[1] Exhibited at the Summer Meeting of the Anatomical Society, Newcastle, 1929.

There is a striking asymmetry of the maxillary air sinuses, the right maxilla being the seat of certain changes not due to any ascertainable pathological process. On the left, the canine fossa is concave, the normal antrum of that side extending forward to the canine ridge and outward into the malar process, though not into the malar bone, nor into the hard palate. On the right, the canine fossa is markedly convex, being filled out by an unusually large antrum which extends both forwards past the canine ridge and medially well into the palatine process, reaching quite to the mid-line in the anterior palatine region, and thereby conferring upon the nasal aspect of the hard palate a bulging convexity in place of the customary concavity. The nasal surface of the right maxilla has a greater concavity than has its fellow, the inferior meatus being consequently unduly wide on that side: the nasal septum suffers no deviation from the median plane.

In the cervical spine certain incipient though definite changes have occurred, indicative of a disturbance of pituitary activity, and which, if further developed, would reproduce exactly the features characteristic of this part of the vertebral column in the acromegalic subject. These changes, like those in acromegaly, constitute the expression of an abnormal response on the part of the skeletal tissues to the mechanical stimuli of stress and strain, and consequently affect mainly those parts concerned in the support and transmission of weight, taking the form of an irregular general hypertrophy. Thus, the vertebral bodies show an increased depth and width, with a characteristic exaggeration and out-splaying of their neuro-central apophyses; the articular pillars are massive (those of C.V. III being relatively enormous) as are their posterior tubercles; the articular facets are increased in area and altered of outline, whilst the intervertebral foramina have suffered some change of size and shape (see fig. 4).

From the posterior aspect of the cervical column, the tips of the transverse processes are invisible owing to the increased girth of the articular pillars; in this respect the specimen resembles the acromegalic, and differs from the normal, spine wherein the vertebral width taken between the extremities of the transverse processes definitely exceeds that taken across the articular pillars.

Apart from the changes described, there is no sign of disease in the cervical vertebrae, whose articular processes are well formed and clean cut.

(*b*) *General*

In the human subject the true craniopharyngeal canal is a rarity, as may be seen from Table I. Le Double's (4) statement that it may be found in some 10 per cent. of new-born children is very suspect; this figure is much too high, and serves only to emphasise the need for precision in terminology and for caution in distinguishing the actual canal from the relatively common vascular foramina of the sphenoidal body and from the gap between pre- and post-sphenoid so characteristic of the macerated sphenoid of the infant and young child.

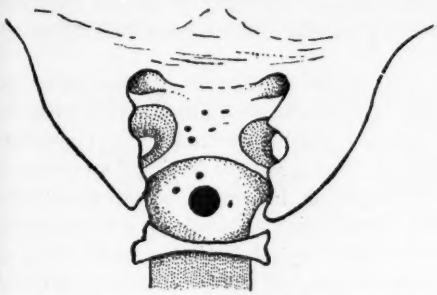

Fig. 1. Cranial mouth of craniopharyngeal canal and associated minor vascular foramina.

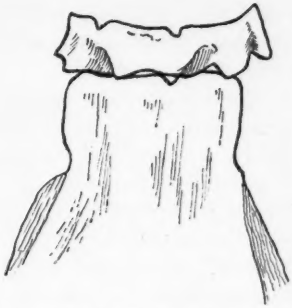

Fig. 2. The condition of the dorsum sellae.

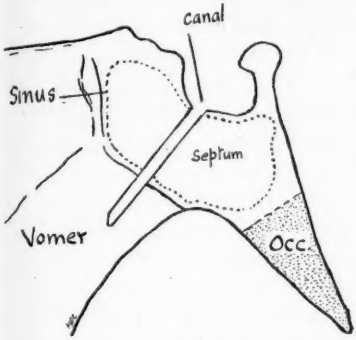

Fig. 3. The relations of the canal (from a skiagram).

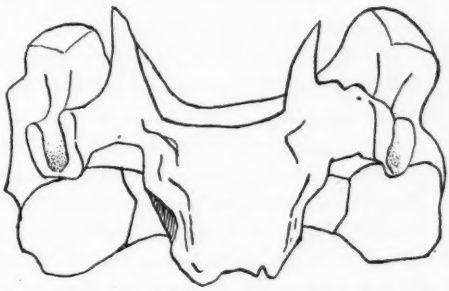

Fig. 4. The condition of the IVth cervical vertebra.

Table I. *Crania specifically examined for craniopharyngeal canal*

Observer	No. of crania examined (adults)	Canal found in
Romiti	800	0
Rossi	3712	9
Le Double	317	1
A.J.E.C.	105	0
Total	4934	10=0·2 %

In character, the canal may be either (*a*) complete, containing a prolongation of dura which blends with the periosteum clothing the under surface of the sphenoid (as in Romiti's case from a 5-year-old girl), or (*b*) incomplete, containing a dural *cul de sac*, with or without pituitary contents, and terminating in the body of the sphenoid or in the posterior part of the nasal septum. Suchannek (10) reported one such incomplete canal filled by a solid epithelial

plug from a 4-year-old child. When the canal presents an inferior opening, that aperture is usually situate about 1·5 mm. behind the postero-superior angle of the vomer.

Most interesting, perhaps, and not devoid of clinical significance, is the association of the ventral extremity of the craniopharyngeal canal with the vomer, in or near which the canal may end. Such a termination is in complete accordance with embryological findings, Prof. Frazer (1) having demonstrated that the pituitary stalk, during development, becomes associated with the posterior border of the nasal septum, down which it travels for a considerable distance. As far back as 1888 Killian had observed that a small mass of pituitary tissue may occur in the naso-pharynx, and in 1909 Haberfeld (2) found this mass (about the size of a rice grain) to be constant in the human subject, lying immediately behind the upper end of the posterior edge of the septum. Erdheim is quoted by Sir Arthur Keith (3) as having discovered this pharyngeal pituitary remnant in each of a series of over fifty bodies examined for its presence, whilst Keith himself (3) has figured much the same condition of things from a 15-month-old child.

That tumours may arise from pituitary remains in this situation is sufficiently well established and calls for no comment here.

CRANIOPHARYNGEAL CANAL IN ANTHROPOIDS

As might be expected from the nature and morphological value of this structure, the craniopharyngeal canal may be traced as a normal or as a variant cranial character from such lowly vertebrates as the ganoids and sharks throughout the higher forms to man himself, although, indeed, large gaps exist in the data available for the different intervening groups. Even among the mammalia no extensive systematic search appears to have been made regarding its incidence, references to its presence being few and scattered.

According to Leche (5) the hedgehog exhibits a persistent pituitary stalk whose ventral (anterior) extremity frequently enlarges to form an independent extracranial bud of tissue, not unlike the condition occasionally obtaining in the human subject. As an anomaly, the canal has been described in the cat by Romiti (8) and in the dog by Le Double (4); the hare and rabbit possess it normally, though in other rodents it occurs as but an uncommon variation, having, as such, been recorded in the adult cavy by Maggi (6) and in *Hystrix cristata* by Le Double. Information concerning primate mammals is of the scantiest. The last author met with the canal in *Cercopithecus sabaeus*, but as regards anthropoids, Maggi's (7) findings, from a specific examination made in 1891 of fifty-seven anthropoid crania are those most commonly quoted; to these no recent addition seems to have been made—certainly the extensive bibliography on anthropoid literature given in 1924 by Sonntag (9) contains no reference to further papers on this subject.

Maggi's findings are embodied in Table II, together with the results of a recent critical investigation of a much wider range of anthropoid and primate

material (see Table II), from the Hunterian Museum of the Royal College of Surgeons and from the Institute of Anatomy, University College, London[1].

Table II. *Craniopharyngeal canal in primates and anthropoids*

Observer	Species	No. examined	Canal found in	%
Maggi	Chimpanzee	5	4	80
,,	Gorilla	10	6	60
,,	Orang	42	9	21·4
A.J.E.C.	Chimpanzee	56	36	64
,,	Gorilla	57	20	35
,,	Orang	44	6	14
,,	*Hylobates* sp.	5	1	—
,,	Catarrhines (various)	13	3	—
,,	*Macacus rhesus*	3	1	—
,,	*M. fascicularis*	2	0	—
,,	*M. nemestrinus*	1	0	—
,,	*Cercopithecus sabaeus*	1	1	—
,,	*Papio hamadryas*	1	1	—

Twenty-six adult skulls of lower primates were carefully examined, and 157 anthropoid crania, the latter including animals of various "races," of both sexes, and of all ages from 2 months' old babies to aged adults. In every specimen examined, the calvaria had been removed and both aspects of the basis cranii were critically scrutinised, the greatest care being taken to distinguish the true craniopharyngeal canal from the vascular foramina in the pituitary fossa. Frequently both cranial and pharyngeal mouths of the canal could be determined, or the passage proved to terminate in the sphenoid or in the nasal septum: all doubtful cases have been rigorously excluded.

Neither age nor sex appears to have any direct bearing upon the incidence or the features of the canal, which is seen to be much commoner in the orang than in man, three times more common in the gorilla, and commoner still in the chimpanzee.

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[1] I desire to thank Sir Arthur Keith and Prof. G. Elliot Smith, F.R.S., for so generously placing this material at my disposal.

THE NON-METRICAL MORPHOLOGICAL CHARACTERS OF THE SKULL AS CRITERIA FOR RACIAL DIAGNOSIS

PART II

THE NON-METRICAL MORPHOLOGICAL CHARACTERS OF THE HAWAIIAN SKULL

By FREDERIC WOOD-JONES
Honolulu

MATERIAL

Most of the osteological material employed in this study is in the collection of the Bernice P. Bishop Museum, to the authorities of which institution I am indebted for permission to examine it. The skulls other than those in the collection of the Museum are such as have from time to time come into the writer's possession and which are lodged in the University of Hawaii. Thirty-two females and thirty males were sexed by a study of their pelves and such other bones of the skeleton as were preserved. The skulls of this series were then examined independently in order to see how far sexual characters could safely be deduced from cranial features alone. From the knowledge thus gained eighteen more female and twenty male skulls were added to the series and these additional skulls were sexed solely on cranial characters, the other bones of the skeleton being absent.

This series of 100 skulls was then examined, careful record was made of the non-metrical morphological characters, and a general description of each skull completed. From these records the occurrence of the non-metrical features is here presented in the form of percentages, and, where importance may attach to it, the sexual incidence is also given.

The great majority of the skulls are from burials that may be termed relatively ancient, and no skull is included in this survey that is under any suspicion of having any of the racial mixture such as is prevalent among the living Hawaiians. Most are from cave burials of the old Hawaiian period and these cave burials are representative of several of the Hawaiian Islands. The Hawaiian is here accepted as being of uniform cranial type in all the constituent islands of the group, for such has been the writer's experience from the examination of a wide series of skulls representative of all the islands. No evidence whatever was found in support of Dixon's claim that there is a "striking" difference between skulls from Kauai and those from Hawaii. Dixon claims that the Kauai crania are of "the Palae-Alpine type" whilst those of Hawaii are "Alpine": but no sort of confirmation of this claim was detected.

Fig. 2. Norma lateralis.

Fig. 1. Norma basalis. Typical male Hawaiian, sexed from the pelvis.

(All figures half natural size.)

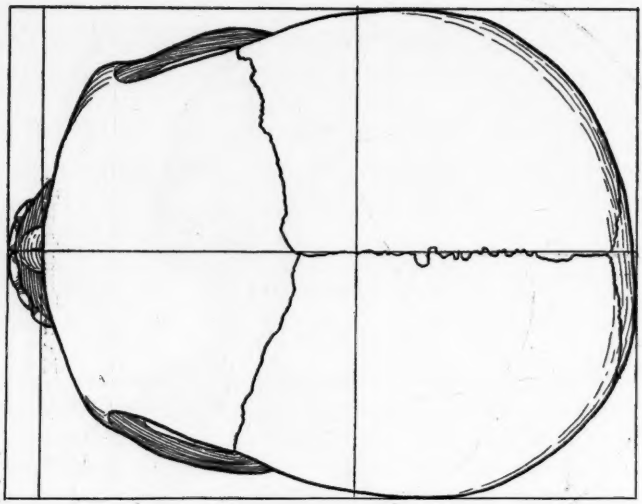

Fig. 4. Norma verticalis.

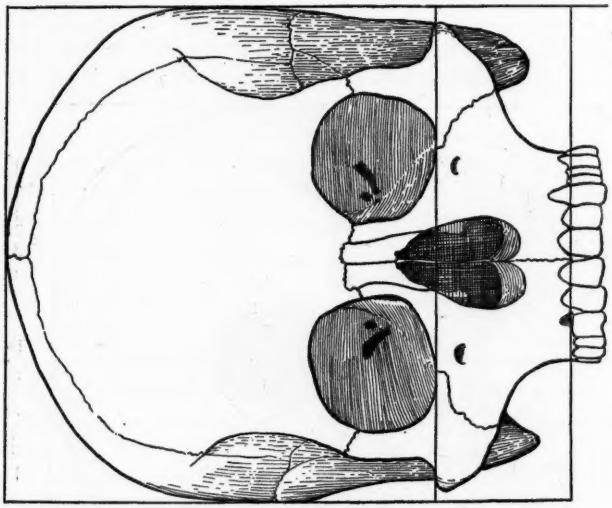

Fig. 3. Norma facialis.

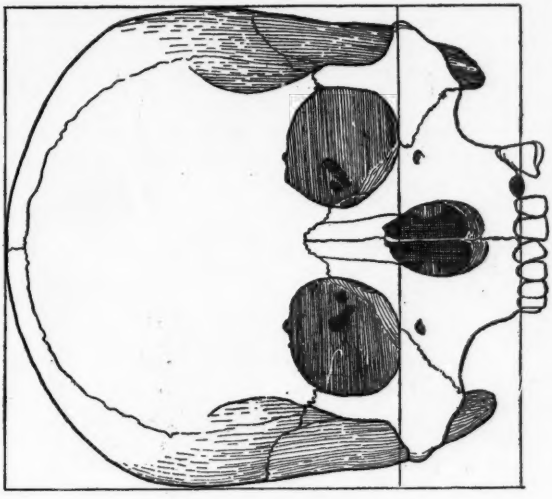

Fig. 6. Norma facialis.

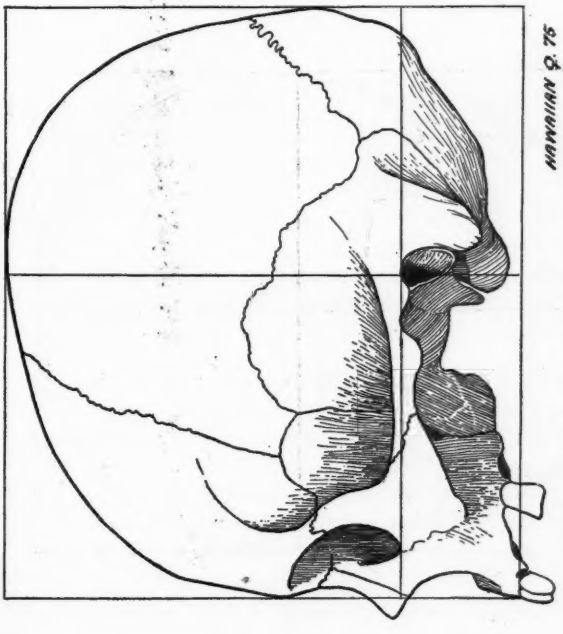

Fig. 5. Norma lateralis. Typical female Hawaiian, sexed from the pelvis.

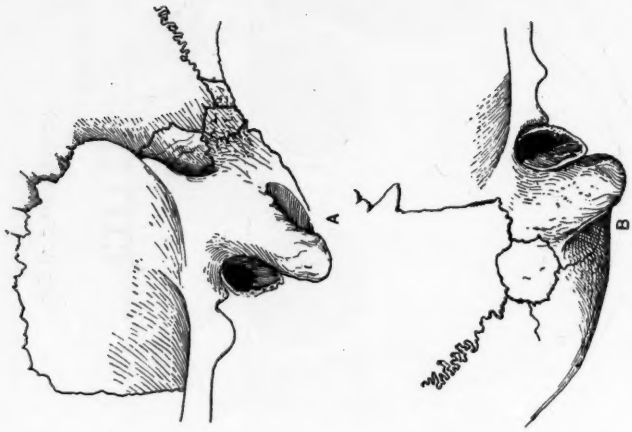

Fig. 8. Common conditions of the occipito-mastoid suture illustrated from Hawaiian skulls.

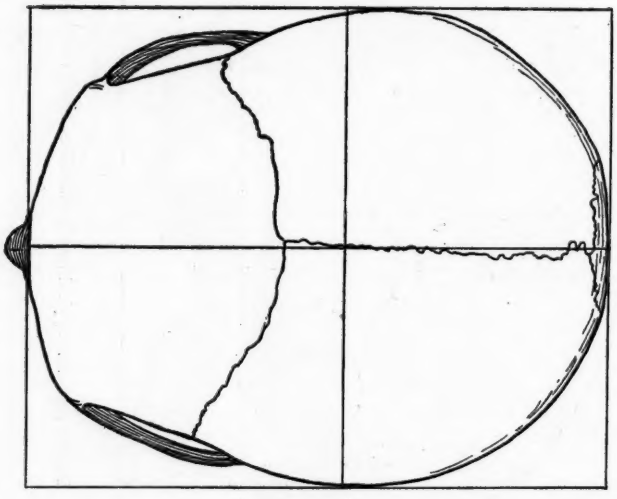

Fig. 7. Norma verticalis.

(1) ***Cranial Form.*** The typical form of the Hawaiian skull, as regarded from the norma verticalis, is a somewhat asymmetrical ovoid most nearly approximating to Sergi's rhomboid; with a shortened and somewhat steeply rising occiput; well-developed parietal eminences and well-filled temporal fossae.

(2) ***Cranial Asymmetry.*** Symmetry and asymmetry are here recorded as the appreciation of these features when the skull is regarded strictly in the

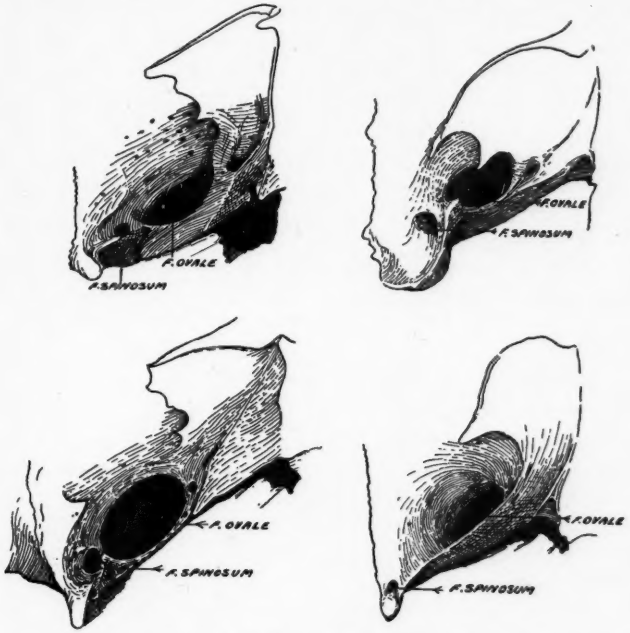

Fig. 9. Minor variations of the region of the foramen lacerum medium, illustrated from Hawaiian skulls.

norma verticalis. No more is meant by these designations than that, when viewed from this aspect, there is an obvious asymmetry in one direction or the other or that no asymmetry is detected by this crude method of estimation.

Judged in this way, only 18 per cent. of the whole series could reasonably be termed symmetrical, and this condition occurred five times as frequently in the females as in the males. In those cases (82 per cent.) in which the asymmetry was well marked it was of the normal type, with left occipital and right frontal bulging, in 65 per cent. (77 per cent of males and 53 per cent. of females): and of the abnormal or reversed type in 17 per cent., the numbers being equal in the two sexes.

(3) *The Sutures* in all skulls examined have been of extremely simple type and no special description of any sutural feature is needed.

(4) *Ossa Suturarum* are by no means frequent, and those recorded are for the most part small inclusions such as are only noted in the course of a systematic examination specially directed towards their recording.

Lambdoid ossicles occurred in the whole series in 23 per cent. of cases (13 per cent. in the male and 33 per cent. in the female); all these inclusions were small and no case of a true interparietal, or of an os epactale simulating its presence, occurred. The ossicles were multiple and occurred bilaterally in 10 per cent. of the total series (7 per cent. in the male and 13 per cent. in the female). An ossicle was present only on the right side in 8 per cent. and all the cases were in females: on the left side only in 5 per cent. (7 per cent. in the male and 3 per cent. in the female).

Ossicles in the *occipito-mastoid suture* were present in 16 per cent. of cases, equally divided between the two sexes. In 8 per cent. of the total series these ossicles were present on both sides of the skull, in 5 per cent. on the left side only and in 3 per cent. on the right side only.

Coronary ossicles were recorded in two cases only, both being males: in one case the ossicles were bilateral and in the other confined to the left side. In both cases the ossicle was included in the normal pars complicata.

Only two skulls showed the presence of a *metopic suture*, one was that of a male, the other female.

(5) *Type of the Pterion.* The pterion was of the normal alisphenoid-parietal type in all cases but one. The exception was a female in which on the left side only there was a small temporo-frontal contact doubtfully effected by a fused epipteric bone. In all skulls of the Polynesian group that I have so far examined this is the only reversal of the pterion that has been present. In only 8 per cent. was the alisphenoid-parietal contact as narrow as 5 mm.

(6) *Epipteric Bones.* Epipteric bones, either unilateral or bilateral, were present in 24 per cent. of cases (29 per cent. in the case of female and 19 per cent. in the case of males). In only one-quarter (6 per cent. of the total series) of these cases were the ossicles bilateral with any approach to symmetry. Of the asymmetrical cases (18 per cent. of the total) the ossicle was present on the left side twice as often as the right in females and on the right side four times as often as the left in males. In the total series right-sided ossicles preponderated over left-sided ossicles in the ratio of 6 to 5.

(7) *Supra-orbital foramina, Notches and Grooves.* Bilateral notches were present in 52 per cent. of all cases; the frequency being as high as 64 per cent. in the males against 40 per cent. in the females. Bilateral foramina were present in 23 per cent. of all cases: in 16 per cent. of males and 30 per cent. of females. At times the condition varies on the two sides. There may be a notch on the right and a foramen on the left (12 per cent. of all cases: 21 per cent. of females, 3 per cent. of males): or the notch may be on the left and the foramen on the right (13 per cent. of all cases: 16 per cent. of males, 10 per cent. of females).

Accessory foramina (f. frontale) are frequent, being present bilaterally in 30 per cent. of all cases (23 per cent. of males and 37 per cent. of females); on the right side only in 13 per cent. of all cases (males and females equal): or on the left side only, a condition occurring in only four skulls, all being females.

Grooves upon the frontal bone of varying degrees of distinctness are by no means uncommon but, owing to the difficulty of defining any criterion by which they may be estimated, no attempt has been made to record their actual numerical occurrence.

(8) *The Anterior Ethmoid Canal.* In no case did the anterior ethmoid canal penetrate the lamina perpendicularis of the ethmoid. In the whole series, 60 per cent. of cases showed the normal sutural exit of the canal and in 40 per cent. it penetrated the frontal above the suture line. In only one case, that of a female, was the condition different on the two sides, the foramen being sutural on the left and in the frontal on the right. The females showed a higher percentage of frontal exits than the males, the figures being 48 per cent. in the female and 32 per cent. in the male.

(9) *The Sutures of the Inner Wall of the Orbit.* In no case was any anomaly detected and fronto-maxillary contact was not approached by extension from either element in any example.

(10) *The Spheno-maxillary Fissure.* The fissure was narrower than that which one is accustomed to consider as normal in the European skull in 45 per cent. of cases. It conformed to the type usual in Europeans in 15 per cent. It was wider than the normal in 15 per cent.; and in 25 per cent., although the medial portion and upper extremity of the fissure were unduly narrow, the lower lateral termination was expanded into a well-marked, often recurved, rounded dilatation. The figures for the two sexes showed exact equality.

(11) *The Form of the Orbit.* In estimating the obliquity of the transverse axis of the orbits, merely by viewing the skull in the norma facialis, it is recognised that only the roughest sort of approximation to accuracy is attained; nevertheless the variations of apparent obliquity of the orbital axis are extremely striking when different racial types are reviewed. In general the Hawaiian orbit is oblique. Obvious obliquity was present in 75 per cent. of all cases, the remaining 25 per cent. showing orbits that may be described as being approximately level. It is rather a curious fact that apparent obliquity is often more pronounced upon one side of the face than on the other. In this series the degree of obliquity of the axes of the two orbits was estimated as approximately equal in only one-third of the cases in which obliquity was present. In the remaining two-thirds of the oblique cases the right orbit was apparently the more oblique six times as often as the left. No significant sexual difference was shown.

(12) *The Infra-orbital Canal.* The canal is typically single; at times there may be a minute accessory foramen, usually to the medial side of the main foramen. Real duplication of the canal in its pithecoid condition is not common and in no case was bilateral. In the whole series the canal was single in 71 per

cent. of cases; a small accessory foramen was present in 23 per cent. and doubling on one side or the other occurred in 6 per cent. In these cases the doubling was twice as frequent on the right side as it was on the left. The female showed the greater number of accessory foramina (27 per cent. females against 20 per cent. males).

(13) *The Form of the Jugal.* Subdivision of the malar bone occurred in none of the skulls included in the type series. In the case of four female skeletons removed from a cave in Oahu an interesting condition was present, for in every skull there was some anomaly of the zygomatico-jugal suture, with an attempt at partial subdivision of the jugal. These burials were recent, portions of clothing attached to the skeletons showed modern stamped buttons and inferior European textiles. Mongolian admixture was almost certainly present.

The malar is of only moderate size: typically its lower margin is only very slightly everted, most cases falling within the class we have defined as parallel. High degrees of concavity of the maxillae are rare; the typical maxillary surface being flat or gently concavo-convex in the lateral direction.

(14) *The Nasal Bones* are typically narrow at their upper extremities. In the majority of cases here classed as narrow, the total breadth across the two bones at the nasion may be assumed to be considerably under 10 mm. With such a definition 76 per cent. of the cases fall within the narrow group. Inequality in size of the upper extremities of the two bones occurred in 50 per cent. of all cases and the right bone was broader than the left twice as often as the reverse condition. In 15 per cent. of cases the upper extremities were synostosed in some degree. This condition was only recorded in the male and it occurred only in the skulls of more aged persons.

(15) *The Narial Aperture* is best described as pyriform in shape and as medium (25 mm.) in breadth. The narial margins are typically double. Both margins are, as a rule, well defined and the outer margin tends to be sharper and more distinct than the inner. Such a condition occurred in 72 per cent. of the total series. The female exhibited greater variability than the male, 80 per cent. of males showing the typical condition against 64 per cent. of females. The divergence of the two margins was carried to an approximation of guttering in 10 per cent., the sexes being equal in this regard. A single margin that was not typically sharp and did not culminate in a nasal spine was present also in 10 per cent., occurring twice as often in the women as in the men. A single sharp margin was found in 8 per cent. and was three times as numerous in women as in men. Apparent subnasal prognathism is generally evident, but it is of a slight or only moderate degree.

(16) *Nasal Septum.* This was preserved sufficiently intact for positive diagnosis in only thirty-four specimens. In these it could be termed medial in only two cases. It deviated to the right in nineteen and to the left in thirteen of the thirty-four examples.

(17) *The Foramen Ovale* fell within the limits of the normal in size, shape and position in 58 per cent. of the total series. The normal series of the male

comprised 74 per cent. of the cases, whereas in the female only 42 per cent. could be thus described.

The posterior bar of the foramen was unduly thin or reduced to a mere spicule of bone in 9 per cent. of cases and in all instances the condition was bilateral: it was more frequent in the female in the ratio of 3 to 2. The posterior wall was deficient to a greater or less extent in 8 per cent., this deficiency being bilateral in 3 per cent. and unilateral in 5 per cent. Unilateral deficiency was present only in the females of the series. In one example, a male, the site of the foramen was indicated by the merest notch on the posterior margin of the alisphenoid where this bone bounded a primitive undivided foramen lacerum medium.

The complete foramen was noted as being unduly large in 8 per cent.; 3 per cent. being bilateral and 5 per cent. being unilateral, all on the right side and all in females. It was unduly small in 17 per cent., 13 per cent. being bilateral. The unilateral cases showed no sexual inequality but the left side was twice as often affected as the right. In all cases in which there was irregularity of size there was a compensation due to the presence of a variation of the foramen of Vesalius.

(18) *The Foramen of Vesalius* was present in 28 per cent. of cases upon both sides and the sexual difference was slight (30 per cent. in females and 26 per cent. in males). It was present only on the right side in 7 per cent. (three times as many cases in females as males) and on the left side only in 10 per cent. (twice as many females as males). The foramen was lacking upon both sides in 55 per cent.

(19) *The Foramen Spinosum* was present as a completed bony canal at its normal site in the spina angularis in only 25 per cent. of cases (26 per cent. in the male and 24 per cent. in the female). In no case was it absent bilaterally or unilaterally. In one female example it was of very minute size on the right side: in one male it was subdivided on the right side, and in one male the primitive condition of a foramen lacerum medium existed on both sides with only a slight notch to determine the site at which the arteria meningea media had entered the cranial cavity. In 44 per cent. of all cases (38 per cent. in the male and 50 per cent. in the female) the canal was more or less incomplete on both sides. In 16 per cent. (sexes equal) it was incomplete on the right side and complete on the left, and in 15 per cent. it was complete on the right side only.

(20) *The Spina Angularis Sphenoidei* is typically prominent. When present as an isolated spine it is practically always in the form of a sharp spicule of bone with a roughened lower edge. More frequently, however, it is present as the culmination of a rough ridge and is of linear form with a roughened lower margin.

(21) *The Laminae Pterygoidei* of the Hawaiian skull are noteworthy for the great development and the wide splaying of the lamina lateralis. In the skulls of some races the lamina lateralis exceeds the lamina medialis only slightly—in the Hawaiian the disproportion is conspicuous.

Commonly the lower free margin is of relatively great length (20 mm. and more), the depth of the plate diminishing rapidly to its upper attached border. In 4 per cent. it was noted that the lateral process was abnormally widely everted even for the Hawaiian series. In 8 per cent. an attempt at the completion of a pterygo-spinous bar was present, this occurred equally frequently on the right and left sides but in no case was bilateral. In every case the bar passed medial to the foramen ovale.

(22) *The Jugular Foramen* was equal in size upon the two sides in only 6 per cent. The foramen on the right side was considerably larger than that on the left in 80 per cent. and the reverse condition was found in 14 per cent. The only sexual difference was found in the case of the larger left-sided foramen which was six times as frequent in the female as in the male.

(23) *The Tympanic* forming the floor of the mouth of the external auditory meatus is of its normal thickness or somewhat more than its normal thickness in 57 per cent.; 32 per cent. being marked as normal and 25 per cent. as being perhaps rather more massive than is the rule in European skulls. In 43 per cent. it was distinctly thin at its lateral margin.

(24) *The Foramen of Huschke* was present in only 3 per cent. In those cases in which it was encountered it was of moderate size and it was present on both sides.

(25) *The Styloid Processes* were present in 87 per cent. of cases: they were well developed in 37 per cent., small in 35 per cent. and rudimentary in 15 per cent. In 13 per cent. they were absent altogether and this condition was three times as frequent in the female as in the male.

(26) *The Posterior Condyloid Foramina* are usually present and are of fair size. In only one case in which they are bilaterally present are they noted as having been conspicuously less than the average size. Well-developed foramina were present bilaterally in 59 per cent. of all the skulls (54 per cent. in males, 64 per cent. in females). They were completely lacking in 17 per cent. of all cases (20 per cent. in males and 14 per cent. in females). A single foramen was present on the right side only in 16 per cent. (23 per cent. in males, 9 per cent. in females): and on the left side only in 8 per cent. (3 per cent. in males and 13 per cent. in females).

A REPORT ON THE NATURE OF CERTAIN BONY SPURS ARISING FROM THE DORSAL ARCHES OF THE THORACIC VERTEBRAE

By L. R. SHORE, M.A., M.B., M.R.C.P., D.P.H.
University of the Witwatersrand, Johannesburg

It is the purpose of this paper to draw attention to certain bony spurs that may commonly be observed projecting from the dorsal arches of the vertebrae of the thoracic region in Bantu skeletons.

The description of a specimen will perhaps serve to focus the reader's attention and to simplify discussion.

SPECIMEN I

This specimen, probably the seventh or eighth thoracic vertebra, is viewed from the right inferior aspect in fig. 1. Two symmetrically placed and pointed

Fig. 1. This figure presents the appearance of Specimen I viewed from the right inferior aspect. The paired bony spurs project from the lower part of the dorsal arch downwards and slightly forwards in front of the inferior articular areas.

spurs project downwards from the antero-inferior aspect of the dorsal arch near the union of the pedicle and the lamina. The bases of these spurs are situated anteriorly and rather medially to the inferior articular facets and are separated from them by distinct intervals. Both spurs taper from base to point, are directed downwards and slightly forwards, and are lightly curved with anterior concavities. The right spur is 9 mm. long and its base is 7 mm.

wide; corresponding measurements for the left spur are 10 mm. and 5 mm. The nearest point of the right spur to the articular surface is 2 mm. and of the left spur 3 mm.

I have not met a description or any mention of such bony spurs in any work on Anatomy, on Morbid Anatomy, or on Pathology save in one only.

Le Double (1) in his *Traité des Variations de la Colonne Vertébrale de l'Homme* describes "une série de petits crochets osseux, qui existaient en dehors de la dure-mère, au niveau des trous de conjugaison du rachis thoracique," and also provides a figure in which the bony processes are indicated by the name "zygantrum."

Fig. 2 presents two tracings in outline only of the figures in Le Double's book and shows, on the left the lateral view, and on the right the inferior view of a thoracic vertebra which bears a paired "zygantrum."

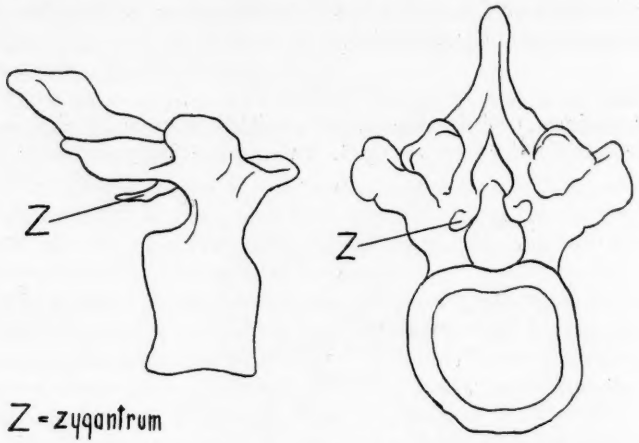

Fig. 2. This figure shows tracings from the figures of Le Double. The tracing on the right is an inferior view and shows the origin of the "zygantrum," *Z*, from the lamina in front of the inferior articular area. The tracing on the left shows the zygantrum projecting down from inferior aspect of the dorsal arch.

These hooks are described, to translate Le Double, as slightly curved on themselves, directed from above downwards and a little forwards, narrower at the tip than at the base, and emplanted on the lower edge of the pedicles about 2 mm. in front of the inferior articular processes.

A comparison of my specimen with Le Double's will leave no doubt that he, applying the name "zygantrum," is describing structures remarkably similar to the bony spurs of Specimen I.

Le Double sets some emphasis upon the origin of the bony processes in front of the inferior articular process, and upon the interval which separates

the bony processes from the inferior articular processes. The detailed analysis of Specimen I and of other specimens will show that the bony spurs of my specimens correspond to Le Double's description in both these points.

It is for the following reasons that my notes on these bony spurs are submitted for publication in this *Journal.*

First, these spurs of bone are not, to my knowledge, described elsewhere than in the writings of Le Double. Secondly, my notes amplify the account given by Le Double, in that the distribution of the bony spurs in the vertebral column of man is recorded from observations made on a series of fifty-one Bantu skeletons. Lastly, the views that I hold as to the nature and the significance of these structures differ from the views of Le Double. That author gives an explanation based on studies in Comparative Anatomy, in particular on certain features of the reptilian skeleton. In my opinion, the bony spurs are more readily to be explained as ossifications in the interlaminar ligaments of the vertebral column.

Analysis of specimen I

The dorsal arch of Specimen I was detached by section of the pedicles, and drawings of the anterior or ventral, and of the posterior or dorsal views of the arch, were then made. These drawings are reproduced in fig. 3, in which the

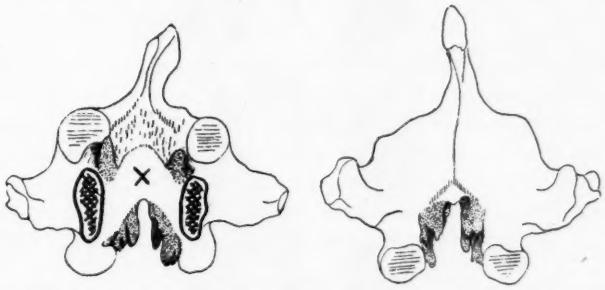

Fig. 3. This figure shows the appearances of the dorsal arch of Specimen I, viewed from the anterior aspect on the left and from the posterior aspect on the right. The "chevron" areas are indicated by *X*, abnormal bone by light stippling, and the cut sections of the pedicles by cross-hatching.

growths of bone in excess of normal are distinguished by light stippling. The attention of the reader is directed to the following findings:

1. The anterior surface of the arch presents a broad band of smooth bone, marked *X*, which is shaped like a chevron with the point directed downwards.

2. This "chevron" area is based on the pedicle on each side, but is somewhat narrower than the pedicle, and is defined in its upper and lower limits by two **V** lines which separate it from superior and inferior areas which are both rough in the texture of their surfaces.

3. The paired spurs arise from the inferior **V** line which limits their bases superiorly, and their most lateral points correspond to where the inferior **V** line blends with the rounded contour of each pedicle.

4. The inferior **V** line lies above the inferior articular areas, consequently the spurs are separated from the articular facets by appreciable intervals. From this and from the last finding it seems that two features of the "zygantrum" emphasised by Le Double are reproduced also in my specimen.

5. The drawing on the right, of the arch from the dorsum, shows that the notch of the vertebral arch between the two superior articular processes is occupied by irregular projections of bone which bear distinct vertical striations.

The clue to the nature of the bony spurs was found during the dissection of the ligamenta subflava in a specimen which comprised the dorsal arches of the lower four thoracic vertebrae and their connecting links.

A drawing of the dorsal arches viewed from the front is reproduced in fig. 4,

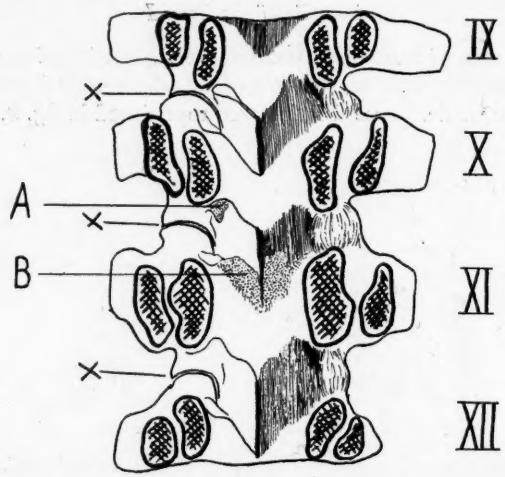

Fig. 4. This figure shows a dissection of the ligamenta subflava in connection with the dorsal arches of the ninth, tenth, eleventh and twelfth thoracic vertebrae. On the right side of the drawing the ligaments and the capsules of the intervertebral joints are shown. On the left side the ligaments have been dissected away and the cavities of the intervertebral joints are exposed. *A* and *B* show ossifications in the ligamenta subflava.

and shows the ligamenta subflava dissected clean on the right and completely removed on the left side of the drawing. The following points are demonstrated:

1. The attachments of the ligamenta subflava are accurately defined in their upper and lower limits by the inferior and the superior **V** lines of adjacent vertebrae.

2. Each "chevron" area, indicated by *X*, is an area of smooth bone which intervenes between the attachments of two ligamenta subflava to each vertebral arch.

3. The inferior attachment of each ligament closely abuts on the superior articular area and, it may be noted, is slightly socketed into the anterior edge of each lamina.

4. The superior attachment of each ligament, on the contrary, is separated by an appreciable interval from the inferior articular area.

I was very fortunate in this specimen, because I found bony processes embedded in the substance of the ligament that connected the tenth and eleventh laminae. These bony processes are indicated, *A* and *B* in fig. 4, and are distinguished by light stippling.

The drawing in fig. 4 shows that the bony processes found in the ligamentum subflavum correspond in position not only with the spurs of my first specimen that project from the inferior **V** line, but also with the exostoses that are based on the superior **V** line.

For the sake of convenience later I propose to refer to the bony processes based on the superior and the inferior **V** lines collectively as ossifications of the upper and the lower vertebral arch.

SPECIMENS II, III AND IV

Fig. 5 presents drawings of three further specimens of vertebrae with bony outgrowths which I interpret as ossifications in the ligamenta subflava. The same essential features are shown in each of these drawings: the "chevron" areas are clear, ossifications of the upper and of the lower arch are based on the superior and the inferior **V** lines, the separation between the ossifications from the inferior **V** line and the articular facet is clear in each case, and ossifications occupy the notch between the superior articular processes.

Specimen II

Twelfth thoracic vertebra. The greatest length of unilateral spur is 11 mm. and it lies 3 mm. in front of the inferior articular facet.

Specimen III

Tenth or eleventh thoracic vertebra. The left spur is 7 mm. long on a base of 8 mm., the right spur is 8 mm. long on a base of 6 mm. The median spur is 7 mm. long and of 4 mm. base width but probably represents an ossification in the interspinous ligament.

Specimen IV

Ninth or tenth thoracic vertebra. The left spur is 13 mm. long, arises from a base of 9 mm. wide and is separated by 4 mm. from the inferior articular facet. The right spur is 3 mm. in length, the base is 4 mm. wide and the separation from the corresponding articular facet is 5 mm.

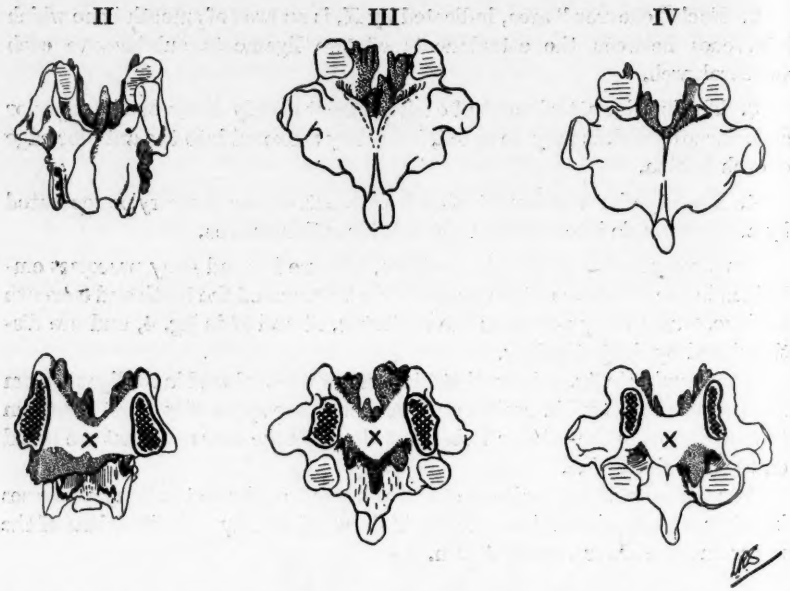

Fig. 5. In this figure are shown drawings of the dorsal arches of Specimens II, III and IV. For each specimen the drawing of the arch viewed from the front is placed under the drawing of the same arch viewed from the back. In each drawing abnormal bone is represented by light stippling, and the sections of the cut pedicles are distinguished by cross-hatching. Note the "chevron" areas in the lower drawings, marked *X*.

DISCUSSION

Le Double explains the occurrence of these processes as a reversion to a condition found in Reptilia. He states that in Crocodilia and certain Lacertilia, notably the iguanas, the neural arch of each vertebra bears a paired wedge-shaped process (zygosphene or zygosphore) on its anterior or cranial aspect. This process lodges in a cavity (zygantrum) excavated in the posterior or caudal aspect of the arch of the preceding vertebra. Some such mechanism of union as a peg and socket is indicated.

If the ossifications we have been considering are indeed atavistic and the ligamentum subflavum represents the zygosphore and zygantrum of Reptilia, it must be remarked that in reversion the mechanism has been inverted. In Reptilia the peg projects from the cranial aspect of the vertebral arch, but in Man the peg projects from the caudal aspect of the arch and the socketing of the ligamentum subflavum, such as there is, is into the cranial edge of the lamina. Further, in the figure in the *Traité des Variations de la Colonne Vertébrale de l'Homme*, the projecting peg is called "zygantrum," which is the term more properly applicable to the socket, as I should conceive.

The upward directed ossifications of the superior arch are not mentioned by Le Double. Consequently their connection with the ossifications from the lower arch have been overlooked. I have met with cases of ankylosis of the dorsal arches in which the ossifications of the upper and the lower arches of two neighbouring vertebrae had coalesced.

In my opinion the bony growths of the superior vertebral arch and the paired processes of the inferior arch are of the same nature, that is to say, they represent ossifications respectively in the lower and in the upper attachments of neighbouring interlaminar ligaments.

Distribution of ossifications of the ligamenta subflava in the vertebral column

Le Double found the structures which he describes under the name "zygantrum" in all of the second to the ninth thoracic vertebrae of a subject aged 50 years. In six vertebrae they were in pairs, and in length they varied from 4 to 12 mm. He also mentions a vertebral column in the Anatomical Museum of the University of Sassari of a man, aged 50 years, in which the third to the eighth and the tenth thoracic vertebrae presented similar processes. Le Double's own specimen and the other he quotes present a common feature in that the distribution of the processes is limited to the thoracic region.

The scanty references might convey the impression that the condition described in this paper is uncommon. In the examination of eighty-two adult Bantu vertebral columns I found that no less than fifty-one possessed spurs from the upper or the lower vertebral arches of the sort I have described, larger or smaller, and differing in the breadth of their distribution in the vertebral column.

To me it is remarkable that ossific processes as common as these are in the Bantu vertebral column have not attracted the attention of anatomists or of pathologists. Ossification of ligaments suggests a pathological process, and indeed I do not dissent from such a view, yet I submit that the structures I describe are worthy of the scrutiny of anatomists for the reasons I have given.

I have prepared a graph to show the distribution in the vertebral column of the bony growths which I interpret as ossifications of the ligamenta subflava. In collecting data for the construction of the graph reproduced in fig. 6, I have noted the presence of abnormal ossifications of any size both in the upper and in the lower vertebral arch. I have allotted an equal value, one small black square, to every vertebra that bears abnormal ossifications above the base line, below the base line or in both positions, according as the ossifications arise from the upper, or the lower arch, or from both arches of the vertebra. In the base line of the graph the designations of the vertebrae are arranged from above downwards as the horizontal line is followed from right to left.

The graph demonstrates the following points:

1. Ossifications are more common in the upper arch, i.e. in the lower

attachment of a ligamentum subflavum, than in the lower arch or in the upper attachment.

2. With few exceptions the site of these bony outgrowths is limited to the thoracic region of the vertebral column.

3. The maximum incidence is at the tenth thoracic vertebra for ossifications of the upper arch, and at the eleventh for those of the lower arch.

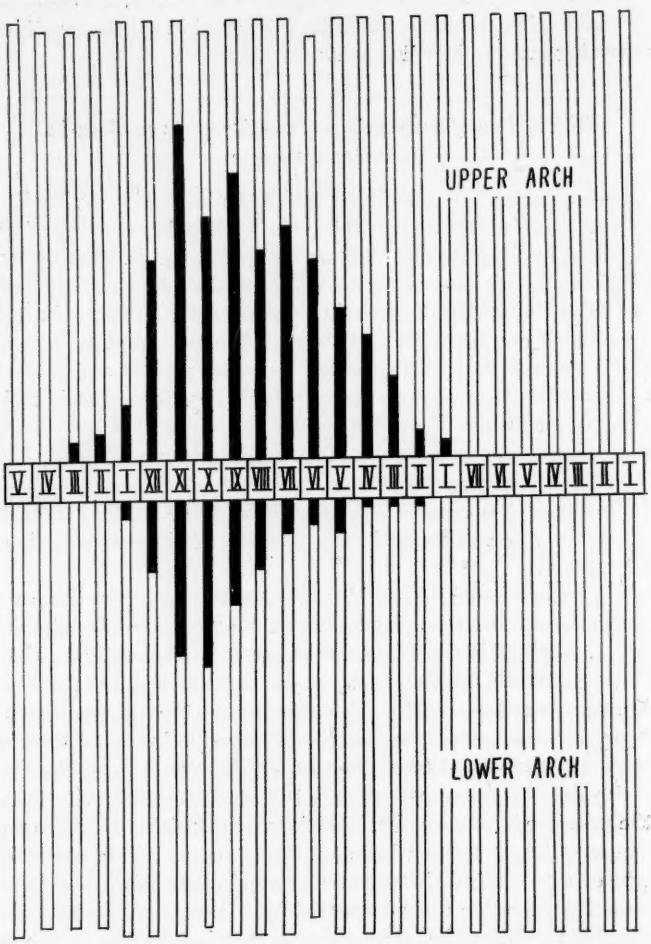

Fig. 6. This figure presents in graphic form the distribution in the vertebral column of ossifications of the ligamenta subflava. Each vertebra bearing abnormal ossifications in the upper arch is represented by a small black square *above* its horizontal designation. Each vertebra bearing an abnormal process from the inferior arch is allotted a small black square *below* its horizontal designation.

The thoracic region differs from the cervical and lumbar regions of the vertebral column in that it presents an anterior concavity when viewed from the side. In this region the superincumbent weight is transmitted through a vertical line which passes in front of the vertebral bodies. Moreover, this vertebral line is furthest removed from the front of the vertebral bodies in the middle of the thoracic series and least at the second and twelfth vertebrae, which lie in the same vertical line, according to Humphry (2).

Such an arrangement must tend to tilt the thoracic vertebrae, in such a way that there is a tendency for the vertebral arches to separate and for the vertebral bodies to be approximated. If strain is a factor in the determination of the process of ossification to a particular ligament, then strain will readily account for the determination of ossification of the ligamenta subflava to the thoracic region, because any tendency for the vertebral arches to separate is resisted by these ligaments.

Also, strain in the ligamenta subflava is greatest at the most concave part of the thoracic curve, and therefore the incidence of ossifications should be highest in the middle of the curve and lowest at the two ends.

In the cervical and lumbar regions, which are regions of anterior convexity, the weight is transmitted by a vertical line which falls behind the vertebral bodies. The tendencies in these regions is for the vertebral arches to fall together and to bring about relaxation of the ligamenta subflava, and for a tension to be thrown rather on the anterior ligaments of the vertebral bodies.

These speculations receive support from the distribution of ossifications shown in fig. 6. The point of maximum incidence of ossification of the ligamenta subflava shown in fig. 6 and the point of maximum concavity of the thoracic curve, which, according to Humphry, is at the seventh or eighth vertebra, do not coincide exactly though the general correspondence is evident. This discrepancy may perhaps be accounted for by the postural changes in the vertebral column which come about with the pathological changes which accompany ossification of the ligamenta subflava.

Associated pathological changes

It is not the purpose of this paper to describe the pathological accompaniments of ossification of the ligamenta subflava. It will be sufficient to state that the vertebral columns which exhibit this condition frequently exhibit also osteo-arthritis and irregular bony fringes from the upper and lower margins of the vertebral bodies. Indeed, to meet a single vertebra in which all three of these conditions coexist is not an uncommon event.

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A CASE OF AN ABNORMAL HYO-BRANCHIAL SKELETON IN *SALAMANDRA MACULOSA* (LAUR.)

By ERIC T. B. FRANCIS, B.Sc. (Lond.)
Student Demonstrator, Zoology Department, University of Reading

The abnormality described below was discovered during an investigation of the general anatomy of the common Spotted Salamander. The work has been done in the Zoological Laboratory of Reading University under the direction of Prof. F. J. Cole, F.R.S., to whom I am greatly indebted for advice and criticism.

The salamander possessing a rather interesting modification of the normal hyo-branchial cartilages was an adult female of the variety *taeniata*, 138 mm. long, which had, some six weeks previously, given birth to 25 young, and was therefore a fully mature individual.

On the left side, the first radial of the copula (representing the remains of the hypo-hyal), instead of occupying the normal position and pointing in an antero-dorso-lateral direction to become more or less imbedded in the substance of the tongue, protruded directly anteriorly in the plane of the copula. At about a millimetre distant from it, dorsal to the expanded end of the cerato-hyal, was a small cartilaginous knob imbedded in a strand of tough connective tissue connecting the anterior border of the cerato-hyal with the hypo-hyal. (N.B. In the figure the cerato-hyals have been displaced lateralwards from their normal position for the sake of clearness; their expanded anterior ends normally underlie the radials of the copula.) The posterior radial on this side was attached rather more anteriorly than the normal position. Obviously the condition represents a partial retention of the larval connection between the cerato- and hypo-hyalia on the left side. The right side was entirely normal.

On both sides, posterior to the second hypo-branchial cartilage, an extra cartilaginous bar occurred. That on the left was fused homo-continuously (i.e. without a break) with the second hypo-branchial cartilage at both ends, but arching away from it in the centre, the space between the two being closed by a membrane in a similar manner to the space between the first and second hypo-branchials. On the right the cartilage in question consisted of a bar of cartilage joined laterally to the second hypo-branchial hetero-continuously (i.e. with a break), and running more or less parallel with it for about half its length, when it ended abruptly. It was separated from the second hypo-branchial by a narrow strip of tough, fibrous connective tissue. There was no sign of muscle remains in contact with them. The connections between the first and second hypo-branchials and the copula were hetero-continuous, while the

junctions between the second hypo-branchials and the first cerato-branchials were homo-continuous with the line of fusion indicated on the left side. The fusions of the hypo- and cerato-branchials of the first arch were homo-continuous, but the points of junction were visible as a faint opaque line. No other relevant abnormality was noticed in the specimen except that the "third" (morphological fifth) arterial arch was unusually robust, its diameter being comparable with that of the pulmonary and common carotid arches.

It seems difficult to avoid the conclusion that the extra posterior cartilages represent the hypo-branchials of the third branchial arch.

I have been unable to trace any mention of a similar case in the literature of the subject. Kallius (1) mentions one case of a third hypo-branchial occurring in the *larva*, and Drüner (2) mentions two such cases. Fürbringer (3) quotes Drüner's work and reproduces his figures. Gaupp (4) makes no original observation but gives an excellent summary of the cases cited by Kallius and Drüner as follows: "Von besonderem Interesse ist das gelegentliche Vorkommen eines als rudimentäres Hypobranchiale III zu deutenden Knorpelstückes, das sowohl Kallius wie Drüner bei Salamandra mac. beobachteten. Kallius fand es einmal auf der linken, Drüner zweimal auf der rechten Seite. In allen Fällen war nur das laterale Ende des Hypobranchiale ausgebildet: in den beiden Drünerschen Fällen lag es als kleines Knorpelstückchen der Verbindung des Hypobranchiale II mit dem Keratobranchiale II an, in dem Kalliusschen Fällen schloss es sich dem medialen Ende des Keratobranchiale III an und war gegen die Copula hin gerichtet, ohne dieselbe jedoch zu erreichen. Dass es sich hier in der Tat um ein rudimentäres Hypobranchiale III handelt, kann wohl nicht zweifelhaft sein." Helena Tarapini (5) finds in a 30 mm. larva of *Salamandra atra* two small cartilages which she regards as rudimentary third hypo-branchials. She regards the case as unique in having a *pair* of rudiments.

The present case, therefore, seems to be of especial interest in that it would appear to be not the persistence after metamorphosis of a *normal* larval structure, but the retention and development in the adult of a condition very uncommon in the larva.

The suggestion that these cartilages may be a teratological duplication of the second hypo-branchials would seem to be negatived by the hetero-continuous junction on the right side, and by the appearance of the space between the cartilage and the hypo-branchial II on the left side being strictly comparable with the corresponding space between the first and second hypo-branchials.

The possibility that they represent persistent cerato-branchials of the second gill arch must not be excluded, in view of the fact that Drüner notes that occasionally in large individuals one finds small (about $\frac{1}{2}$–1 mm. diameter) knobs posterior to the hypo-branchial II, which he takes to represent the remnants of the cerato-branchials II to IV. The cartilages in the present case are very much larger than those Drüner mentions, and it seems unlikely that

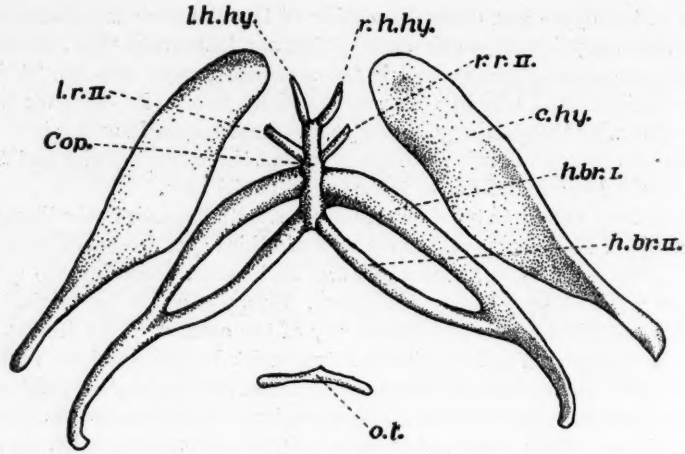

Fig. 1. Normal hyo-branchial cartilages of *Salamandra maculosa*, viewed from the dorsal side. (× 5.)

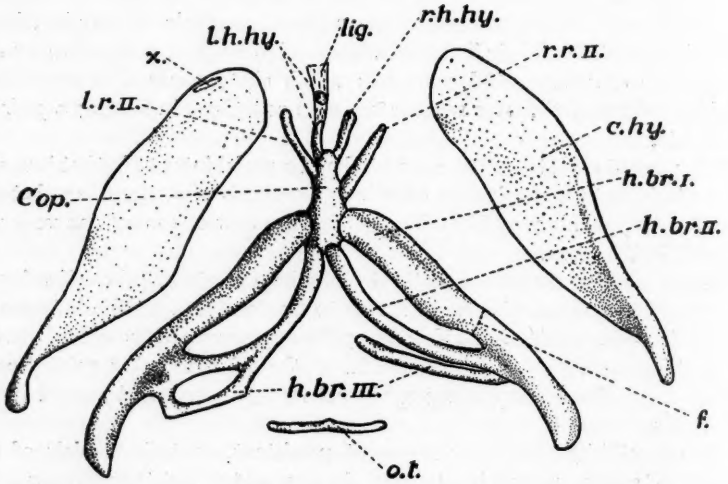

Fig. 2. Abnormal hyo-branchial cartilages of *Salamandra maculosa*, viewed from the dorsal side. (× 5.)

they would have lost so completely the homo-continuous connections with the dorsal end of the cerato-branchial I which they would have had in the larva, and have wandered into such a definite relation with the hypo-branchial of the second arch. The absence of any muscular remains is also against this view.

EXPLANATION OF FIGURES

In both figures the cerato-hyals are shown laterally displaced for sake of clearness; normally their anterior ends overlap one another and lie ventral to the hypo-hyals.

ABBREVIATIONS USED IN FIGURES

c.hy.	Cerato-hyal.
cop.	Copula.
f.	Line of fusion between hypo-branchial I and cerato-branchial I.
h.br.I.	First hypo-branchial.
h.br.II.	Second hypo-branchial.
h.br.III.	Third hypo-branchial.
l.h.hy.	Left hypo-hyal.
r.h.hy.	Right hypo-hyal.
lig.	Ligament attaching the left hypo-hyal to the cerato-hyal in the abnormal specimen.
o.t.	Os triangulare.
l.r.II.	Left second radial of the copula.
r.r.II.	Right second radial of the copula.
x.	Insertion of ligament from hypo-hyal.

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SUPRA CONDYLAR PROCESS

By R. K. RAU, L.R.C.P., F.R.C.S. (Edin.)
AND
D. SIVA SUBRAHMANIAM, M.R.C.S. (Eng.), L.R.C.P.
Department of Anatomy, Medical College, Vizagapatam (S. 1)

Our attention was drawn to an unusual prominence on the front of the lower and of the humerus in a right upper limb, allotted to students for dissection. The idea that it might be the "supra condylar process" occurred to us, and we set to work to verify this. The left limb of the same subject was at the time being dissected by other students, and was found to present a similar process. This abnormal condition would therefore appear to be a bilateral one.

DESCRIPTION

The process on the right side is a spur of bone resembling a small vertebral spinous process, about three-quarters of an inch long, and a little over a quarter of an inch at its broadest part corresponding to the base, jutting out from the antero-medial aspect of the humerus about an inch above the level of an imaginary line drawn between the two condyles. It is directed forwards and slightly downwards. The upper and lower borders are very nearly straight, terminating in a rounded blunt extremity. The surfaces are internal and external and nearly flat. A strong fibrous band extends from the tip and upper border of the spur cranio-medially to the well-defined internal intermuscular septum, forming a musculo-fibrous tunnel for the transmission of the neurovascular bundle—comprising the ulnar artery with its vena comites and the median nerve. The interest of this abnormality is enhanced by the existence of the high bifurcation of the brachial artery, which, after giving off the arteria profunda brachii and the superior ulnar collateral arteries (both the profunda arteries) is seen to fork out into the radial and ulnar arteries at about the junction of the proximal with the middle third of the arm. The median nerve passes between the terminal branches of the brachial artery proximally and later accompanies the ulnar artery, lying at first lateral and then anterior to the artery. The two structures pass under cover of the fibrous band resting on the medial surface of the process, and then descend distally vertically, the nerve pursuing its usual course between the humeral and the ulnar heads of the pronator radii teres. The pronator teres has a distinct third head of origin from the process and the fibrous band attached to it. The median nerve is here found to give off the lateral cutaneous branch of the forearm in the proximal part of the arm, while the musculo cutaneous nerve is seen ending in the substance of the brachialis anticus.

The process on the left side is slightly larger than that on the right, springing from a little over an inch above the lower end of the humerus. It is about seven-eighths of an inch long and three-eighths of an inch broad at its base. It also terminates in a blunt extremity. The superior border is convex, and the inferior concave. The lateral surface is nearly flat, while the medial surface shows a shallow groove for the lodgment of the brachial artery and the median nerve.

DISCUSSION

We have specially looked for this process in more than two hundred macerated bones in the ossuaries here and in Madras, but without success. During an experience of some ten years we have encountered this abnormality only on the one occasion, and are inclined to think, therefore, that it must be a rare one. In Piersol's *Anatomy*, Dr Dwight says that the process occurs "probably in two or three per cent." Ernest Frazer is of the opinion that it is found "now and then." Other authorities also refrain from stating any exact figure in regard to the frequency of the incidence of the process. The apparent rarity of the abnormality, and the paucity of literature on the subject, appear to us to be some excuse and justification for this article.

MORPHOLOGY AND PHYSIOLOGY

The entepicondylar foramen has been described to be a defect of ossification, situated above the inner epicondyle of the humerus for the transmission of the median nerve. In the archaic reptile *Sphenodon* an additional ectepicondylar foramen for the musculospiral nerve is said to exist on the outer side. The foramen edentata has a foramen above the inner condyle. In the carnivora there is a supra condylar in cats, and some other groups, but not in dogs or bears. It is, however, present in the insectivora, in many of the New World monkeys, and in most lemurs. In men and the higher apes (anthropoid) the foramen above the inner condyle is generally absent. The process occasionally takes the place of the foramen in man. Dwight mentions a solitary instance of the occurrence of a foramen in man. When present it is regarded as atavistic structure—a reversion to the ancestral condition found in many orders of mammalia. It has been ingeniously suggested that the shaft of the humerus between the two foramina met with in *Hatteria* and the bars bounding the foramina on each side represent the three fin rays of the pectoral limb of the fish. The arch thrown across the neuro-vascular bundle, or only the nerve in some cases, is perhaps the homologue of the foramen found in many animals. It is surmised that the fibrous arch, as in other parts of the body, might have a protective function preventing the compression of the structures during the contraction of the muscles in the front region of the elbow.

SUMMARY

The points of interest are:

1. Bilateral condition and the fairly large size of the processes.

2. Their situation about an inch proximal to the intercondylar line.

3. Their resemblance to the diminutive spines of the vertebrae differing from the "unciform" nature as described in text-books.

4. The origin of the third head of the pronator radii teres on both sides.

5. Co-existence of other abnormalities: (*a*) the high bifurcation of the brachial artery; (*b*) the median nerve giving off the lateral cutaneous nerve for the forearm on the right side.

It need hardly be pointed out that in routine clinical examinations and radiographic examinations of the elbow joint and the surgical exposure of the brachial artery for ligation, the occasional occurrence of the supra condylar process must be borne in mind to avoid errors in diagnosis.

We have to thank Dr D. Sivasubrahmaniam, M.R.C.S., L.R.C.P., Senior Demonstrator in Anatomy, for having brought the abnormality to our notice, and for his assistance in the dissection of the part.

ANATOMICAL NOTES

A CASE OF CONGENITAL ABNORMALITY OF THE HEART WITH APPARENTLY AN UNUSUAL ABNORMALITY OF THE GREAT VESSELS

By C. P. MARTIN, M.B., M.Sc.,
Trinity College, Dublin

THIS case was seen by Dr Hooper, Kenilworth Square, Dublin, and also by Dr A. Parsons of Dublin who demonstrated on it as a case of congenital heart disease. After the post-mortem the heart, arch of the aorta, cardiac ends of the great vessels and both lungs were forwarded to the School of Anatomy, Trinity College, Dublin. The parts had not been separated, but the heart and aorta had been opened at the post-mortem.

The following is a copy of the clinical notes written by Dr Hooper:

"M - - - - - - - F - - - - - - - - born 15 August, 1911, at - - - - - - - - died 26 December, 1929, at - - - - - - - - - being 17 years of age. He first attended me at the age of two, but prior to that his mother had not noticed his colour being abnormal, and was certain his colour was good. His mother used to carry him in her arms into my dispensary. He was suffering from congenital heart disease and the general cyanosis was very marked. As he grew older this blue colour of the skin became deeper, not only his mucus membranes but his tissues were purple. The term 'blue disease' or Morbus Coeruleus was certainly applicable to this case. At the age of 15 his colour was improved, and so much so that in the last few years of his life his parents thought he was getting better. The clubbing of his fingers and toes and the murmur in his heart were also very marked. He grew to be a good height, about 5 ft. 3 in., although he was of a frail and delicate build. He always complained of the cold. He had a splendid appetite. He was a bright intelligent boy, but had a very bad temper. His family history was very good, and he had comparatively little illness during his life. Mild whooping cough at 1½ years and measles at 2 and a slight attack of haemoptysis about a year before he died constituted his illnesses.

"About a week before he died I was called to see him. He had been coughing a lot for about one month and the left upper lobe was crepitating. I then thought he had phthisis, and on St Stephen's Day he got a very severe attack of haemoptysis and died."

Description of the specimen

Viewed from the front the heart appears to be rotated with its anterior surface turned towards the left, and is more vertical than is usual. The anterior surface is formed almost entirely by the right ventricle, and the apical notch is situated exactly at the heart's apex. There is a want of fullness in the region of the conus arteriosus. The ascending aorta is to the right of the stem of the pulmonary artery and not at all behind it, but a transverse groove about 1 cm. deep separates the anterior surface of the right ventricle and the anterior surface of the ascending aorta. The pulmonary artery is very small at its commencement, but enlarges considerably after a short distance. It has very thin walls. Its anterior surface is continuous with that of the right ventricle just to the left of the ascending aorta. The left pulmonary artery is larger than the right. Otherwise the anterior aspect of the heart is normal.

The arch of the aorta curves over to the left in front of the trachea. 4 cm. from the upper margin of the right ventricle three large arteries come off together from the left antero-lateral aspect; 1½ cm. further up one large artery comes off the right antero-lateral aspect, and after a course of 1 cm. divides into two. All these arteries were cut close to the arch of the aorta so their identity cannot be determined. A fine fibrous cord, the remains of the ductus arteriosus, runs from the pulmonary artery just at its bifurcation to the most left of the three branches coming off the left antero-lateral aspect, and what appears to be the left recurrent laryngeal nerve winds round this artery to the left of the ductus arteriosus. So this branch probably is the left subclavian.

To the right of the ascending aorta the superior vena cava can be seen. It was cut 6·8 cm. above the right auricular appendage, almost on a level with the top of the aortic arch. A large vein runs across from left to right below the arch of the aorta and behind the ascending aorta, and joins the superior vena cava (*C* in fig. 1). This vein commences by the junction of two considerable veins 3·5 cm. from the superior vena cava, and joins the latter vessel ½ cm. below the junction of the vena azygos and superior vena cava. Unless this vessel represents the left innominate vein no trace of the latter was found, but it may have existed above where the superior vena cava was cut.

Viewed from behind it can be seen that the aorta passes to the left dorsal to the oesophagus, although it is ventral to the trachea. It is therefore a case of a right aortic arch. Otherwise no abnormality is noticeable from this aspect. The coronary sinus and coronary arteries are normal.

On opening the right ventricle it is seen that the aorta opens out of this cavity at the upper and posterior angle, and the opening is guarded by a valve with three cusps, normally situated. Immediately below the left posterior cusp of this valve is a large aperture in the inter-ventricular septum, which easily admits the top of a thumb. The lower margin of this aperture is somewhat thickened. Running across the lower and anterior edge of the ascending aorta, and corresponding in position with the bottom of the groove described as separating the anterior surfaces of the ascending aorta and right ventricle when viewed from the front, is a strong band of muscle which projects into the ventricle, giving an appearance as if the anterior wall of the aorta had been partly invaginated into the ventricle. This prominent muscle (*A*, *A'* in fig. 1) commences just below and in front of the opening in the inter-ventricular septum and passes upwards, backwards and to the right into the right side of the ventricle. In front of this muscle a small part of the cavity of the right ventricle ascends for about 1 cm. and from the extreme left end of this recess the pulmonary artery opens. The opening of the pulmonary artery is very small, barely admitting a probe of 2 mm. diameter. No valve can be seen in the pulmonary artery. The recess in the ventricle leading to the pulmonary artery is marked *B* in fig. 1.

The thickness of the muscle walls in the right and left ventricles is equal. The atria are normal. There is a small opening in the bottom of the fossa ovalis, but this may be an artifact produced at the post-mortem. The bronchial arteries do not appear to be markedly enlarged, and no trace of any other anastomosis between the pulmonary and systemic circulations was found.

Discussion.

The abnormalities present in this case are therefore as follows: (*A*) A right aortic arch. (*B*) Stenosis of the pulmonary artery. (*C*) An incomplete inter-ventricular septum. (*D*) The presence of an unusual vein joining the superior vena cava.

As regards the cardiac abnormalities the persistence of the inter-ventricular foramen appears to be secondary to the stenosis of the pulmonary artery. Herxheimer states that some defect in the septum must accompany pulmonary stenosis (2). The

latter feature, according to Keith (3,4), arises in the great majority of cases from non-development of the bulbus cordis, and it is to this category that the case described here apparently belongs; it agrees closely with the cases he described and figured as simple non-development of the bulbus. The marked development of the muscle band marked *A*, *A'* in fig. 1 is interesting. It apparently represents the hypertrophied infundibular bands which are described by Keith, and which seem to be part of the longitudinal muscle of the right ventricle as described by Mall(5) and Shaner(7). In cases of incomplete inter-ventricular septum it apparently hypertrophies, and acts by partly closing the inter-ventricular foramen during systole. It seems to be

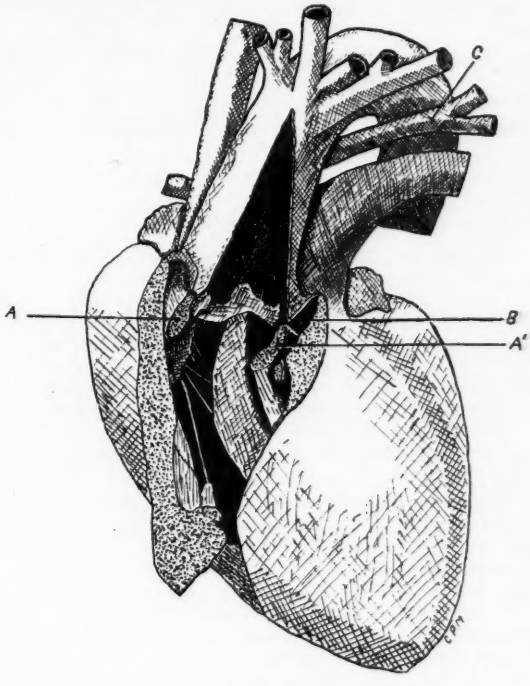

Fig. 1

A, *A'*. Cut ends of enlarged right and left infundibular bands. Behind *A'* is the inter-ventricular foramen.
B. Recess of right ventricle leading to pulmonary artery.
C. Abnormal vein passing behind ascending aorta to join superior vena cava.

present in most cases of deficiency of the septum, but the descriptive literature usually omits any reference to the musculature. But it is apparently present even in some cases of transposition of the aorta and pulmonary artery(1).

In the case now described it is difficult to see how the individual lived so long with so small an opening to the pulmonary artery and no evidence of any enlargement of a collateral circulation. Herxheimer gives statistics showing that these cases mostly die in early life(2). The improvement noticed in this patient at 15 may possibly have been due to general muscular development of the body at about that age leading to the

better development of the heart muscle and especially the infundibular bands mentioned above. Presumably the ductus arteriosus was closed at birth, as otherwise it is difficult to account for its subsequent occlusion. Perhaps the primary abnormality of all is the persistence of a right aortic arch. This conceivably might lead to early atrophy of the ductus arteriosus, as on the right side it normally disappears at an early age, and this again could lead to non-development of the bulbus, or that part of it that is included in the pulmonary artery.

As regards the large abnormal vein joining the superior vena cava, it is very unfortunate that it was cut too short to permit of definite identification. If it is not the left innominate vein, then it is impossible to say what it is. If it is the left innominate vein, then it represents an abnormality that, so far as I am aware, has not been observed hitherto.

The patient died of phthisis. The frequency of phthisis in cases of pulmonary anaemia, and its absence or rarity in cases of mitral disease resulting in pulmonary congestion, suggests that at least one large factor in predisposing to this malady is anaemia, either general or local. It would also suggest that the treatment of phthisis should aim at producing pulmonary congestion.

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A CASE OF ABNORMAL ATLAS AND AXIS VERTEBRA

By U. V. NAYAK, M.B., B.S.
Lecturer in Anatomy, Royapuram Medical School, Madras

Abnormal conditions of the atlas and axis vertebrae are not commonly met with in the dissecting room and constitute an extremely rare anomaly. In this paper is described a case of atlanto-occipital union and fusion of the axis with the third cervical vertebra as found in a South Indian male aged about 50 years. The specimen, now preserved in the museum of the Royapuram Medical School, was accidentally discovered during dissection of the atlanto-occipital and atlanto-axial joints. The condition of the bones clearly showed that it was non-traumatic and non-pathological. It might have been the result of congenital irregular segmentation of the cervical spine or more probably abnormal ossification of the capsular and other ligaments during the period of postnatal growth. Considering the nature and functional importance of the joints in relation to these bones and the disability consequent upon any grave developmental anomaly thereof, the condition is one of rare occurrence and is deserving of special attention.

Description

The atlas vertebra is completely fused with the occipital bone: a groove on the inner aspect of the line of fusion of the anterior arch of the atlas with the margin of the foramen magnum indicates the original separate existence of the atlantal segment of the fused mass. The anterior arch presents on its anterior aspect a prominent tubercle for the longus colli muscles, and on its posterior aspect a circular facet for the odontoid process of the axis. The posterior arch of the atlas is fused with the posterior margin of the foramen magnum, leaving on either side foramina for the entrance of the vertebral artery and the exit of the first cervical nerve. The lateral masses of the atlas are indistinguishably fused with the condyles of the occipital bone. The inferior articular facets of the atlas projecting downwards and medialwards are convex and slightly oval in shape (instead of being, as usual, flattened or slightly concave and circular in outline), probably as an adaptation here for slight nodding movements of the head which normally take place at the atlanto-occipital articulation. On the medial side of these facets the lateral masses present the tubercles for the attachment of the transverse atlantal ligament.

The axis is fused with the third cervical vertebra: the fusion is complete between the bodies and the lateral masses, almost suggesting a condition of assimilation of the third vertebra by the second. The transverse processes of these vertebrae are not fused, indicating that the two segments must have been formed separately and have subsequently fused, but it is difficult to make out at what stage in development the fusion has taken place. The spinous processes having been removed during the progress of dissection, it is not known whether they were also fused. The axial superior articular processes are large in size, oval and concave instead of being as usual convex. The left facet shows a definite lip on its outer side, strongly indicative of an attempt at provision for slight nodding movements usually taking place at the atlanto-occipital articulation. These facets are supported on the body, pedicles, transverse processes and, to a slight extent, on the lateral masses, and immediately behind them is the groove for the second spinal nerve. The lateral masses are completely fused, and, in front, between them and the fused bodies, are the circular intervertebral foramina for the exit of the third cervical nerves. The bodies are so completely fused that no idea of their original separate existence can be made out.

The odontoid process is conical in shape, not sturdy and does not show the prominent tubercles on either side immediately below the apex. The anterior atlantal facet and posteriorly the groove for the transverse atlantal ligament are well marked.

The condition of the other segments of the cervical spine was normal both in number and the arrangement of their parts.

Cases of synostosis of the atlanto-occipital articulation, partial or complete, have been described in the literature, but I do not know whether that condition has been found at any time in association with an abnormal axis[1]. This association no doubt is of anatomical interest only, but functionally not more important than in cases of pure atlanto-occipital fusion.

[1] See article by Prof. G. Elliot Smith, *Brit. Med. J.* 1908, vol. II, p. 594.—Ed.

RECENT APPOINTMENTS IN CHAIRS OF ANATOMY AND ZOOLOGY

Prof. Frederic Wood-Jones, Rockefeller Professor of Physical Anthropology in the University of Hawaii, has accepted the Chair of Anatomy in the University of Melbourne, in succession to Prof. R. J. A. Berry who has resigned his position. Prof. Wood-Jones is already well known in Australia, having occupied the Elder Chair of Anatomy in the University of Adelaide, 1919–1926.

Prof. J. C. Boileau Grant has been appointed to the Chair of Anatomy in the University of Toronto in succession to Prof. J. P. McMurrich. Prof. Grant succeeded Prof. Alex Gibson in the Chair of Anatomy in the University of Manitoba in 1919. He is the author of one paper on "Teaching Anatomy" and four on the "Indians of Canada."

Dr Donald Mainland has been appointed Professor of Anatomy at the University of Dalhousie, Nova Scotia. M.B., Ch.B. (with Honours), Edinburgh, 1925. Appointed Graduate Demonstrator, Edinburgh, 1925; Assistant Professor of Anatomy in the University of Manitoba, Canada, 1927. Investigations on ovarian structure and upon the earliest stages of development in Mammals, including the relationship of this development to Mammalian teratology. Has applied quantitative and statistical methods to histological and embryological material. Awarded the Gunning Victoria Jubilee Prize in Anatomy, Edinburgh University, 1927.

Dr James Ritchie, formerly Keeper of the Natural History Department of the Royal Scottish Museum, Edinburgh, has gone to the Regius Chair of Natural History at Aberdeen in succession to Prof. Sir J. Arthur Thomson who has retired.

Dr F. W. Rogers Brambell, formerly Lecturer in Zoology at King's College, London, has gone to the Lloyd Roberts Chair of Zoology at the University College of North Wales, Bangor, in succession to the late Prof. P. J. White.

Prof. L. T. Hogben resigned the Chair of Zoology in the University of Cape Town, on his appointment to the newly instituted University Chair of Social Biology at the London School of Economics.

Dr T. A. Stephenson, formerly Lecturer in Zoology, University College, London, has been appointed to the Chair of Zoology in the University of Cape Town vacated by Prof. Hogben.

REVIEWS

Röntgenographic Study of the Movements of Abduction at the Normal Shoulder Joint. A reprint from the *Medical Journal of Australia*, 27 July, 1929, pp. 3–4, by H. FLECKER, M.B., Ch.M. (Sydney), F.R.C.S. (Edinburgh), with three figures.

The marked degree of humero-scapular movement after the abducted arm passes the horizontal is illustrated. A table is presented of various angles made by the humerus, scapula, clavicle, etc. Such angular radiographic measurement is of approximate practical value. As implied by the title, the study is exclusively radiographic, but the patient's posture, whether erect, supine, or prone, is omitted.

The results support the papers read by Cathcart before the B.M.A., 1882, published in the *Journal of Anatomy* 1884 (without radiograms), and by Lockhart, *Proceedings of the Anatomical Society*, June 1929, published in the *Journal of Anatomy* 1930 (with radiograms).

The Development and Growth of the External Dimensions of the Human Body in the Foetal Period. By RICHARD G. SCAMMON and LEVY A. CALKINS. (University of Minnesota Press, Minneapolis, 1929.) Pp. xxiii + 367. 73 figs. and charts + 180 tables.

The published work which has appeared from the University of Minnesota in relation to antenatal and postnatal growth under the stimulus of Prof. Jackson and Prof. Scammon has been one of the main features in that broadening of the anatomical horizon which is so welcome. In this large monograph the authors have dealt with the growth of the foetus, as distinct from the ovum or embryo, in great detail and have applied the graphic and analytic methods to a mass of material, consisting of 400 selected foetuses ranging from 2·3 to 54·4 cm. in total or crown-rump length. For each foetus seventy-one external dimensions have been registered. The effects of various fixation fluids on the dimensions of the foetuses have been analysed.

Five major external dimensions have been analysed in detail, viz. crown-heel length, crown-rump length, spine length, crown-umbilicus and crown-suprasternal length. Empirical formulae have been derived for each of these measurements, and when four of the dimensions are plotted against the first, the crown-heel length, the curve is virtually a straight line of the type $M.D. = aL + b$, where $M.D.$ is a major dimension, L the crown-heel length, a a positive constant less than unity, and b a positive constant. Thus all four dimensions undergo a reduction in relative size in the foetal period. Whereas the total or crown-heel length increases sevenfold from 3 months to birth, the four major dimensions increase in this period over a range extending from sevenfold to somewhat less than sixfold.

The growth of the head and neck has been recorded by twenty-two external dimensions, fourteen linear and eight circumferential. All of these when plotted against the crown-heel length show a straight line of the type $H.D. = aL + b$, where $H.D.$ is the external head dimension. The total head and face height forms nearly one-third of the total length at 3 months, about one-quarter at 6 months and slightly less at birth. There is a small, but doubtfully significant, increase in the cephalic index in the foetal period. The cranium is becoming longer and broader in proportion to its height throughout foetal life. The facial portion of the head grows more in height, breadth and even in antero-posterior diameter than does the cranium, and during this period the face becomes a little broader in relation to its length. These

observations on the growth of the face are of great interest as they emphasise the sub-cerebral position of the early foetal nose.

The growth of the trunk has been analysed in terms of twenty-two external dimensions, five circumferential and seventeen linear. The various external dimensions of the trunk increase from seven to nine times from 3 months to birth. The trunk becomes more slender in proportion to body length in the latter part of foetal life. The thoracic indices at the level of the nipples, xiphisternal junction and tenth rib show but little variation throughout the period. The lower part of the thorax grows more rapidly than the upper in all dimensions.

An important section deals with the growth of the pelvis. Four measurements in the transverse plane, one in the antero-posterior and one in the ventral plane, all yield straight lines when plotted against the crown-heel body length. The pelvis grows relatively more rapidly in height, and least rapidly antero-posteriorly.

The growth of the upper and lower limb was tabulated in terms of certain linear and circumferential diameters. The upper limb is one-third of the total body length at 3 months and about two-fifths at birth. The lower limb undergoes a marked increase; and this is more marked in the leg than in the thigh. For both limbs the plotted curve is of the type $E = aL + b$, where E is the external dimension of the limb, and b is a negative constant. The upper and lower limbs are of equal length at the stage when the crown-heel length is 7 cm., late in the third foetal month.

The main value of this monograph is the illustration of the extent to which the linear growth of the various parts of the body maintains a uniform ratio, so that the curve is of the form $y = ax + b$, with but slight changes in value of b from positive to negative, whenever any external dimension is plotted against total length. The abstracts of previous studies on quantitative data in relation to early human growth are invaluable and the bibliography is excellent. This monograph deserves to stand alongside those of Quetellet and Vierordt and one cannot but express one's admiration and thanks for such a wealth of material.

Histology for Medical Students. By H. Hartridge, M.A., Sc.D., M.D., M.R.C.P., F.R.S. and F. Haynes, M.A. (Humphrey Milford, Oxford University Press.) 1930. Pp. 369. 512 figs. 15*s.* net.

Text-books of histology giving an adequate account of the subject suitable for medical students are remarkably scarce; therefore a new book designedly written for this class of reader arouses particular interest, especially when it possesses 502 illustrations, all original and nearly all in colour. But the majority of the illustrations can be very nearly covered by two postage stamps; low power views of this size cannot be drawn or reproduced with sufficient fineness of detail, and when the magnification is higher the field is extremely limited. The few large microscopical figures are excellent. A number of the illustrations are diagrams—here again the usefulness of many is impaired by their small size; most of the larger diagrams are rather crude, more in keeping with the informality of the blackboard than with the dignity of a text-book.

The text in general contains an unusually complete, straightforward account of histological structure, but unfortunately contains also a surprising number of errors such as the following. On pp. 103–4 it is stated that the coronary vessels have no vasomotor nerves and the cerebral arterioles probably none. On p. 106 "the so-called adenoids" are said to be "on the upper surface of the soft palate." The pons is twice described (p. 138 and p. 144) as being formed round the front of the mid-brain. Continuity of the meninges with the nerve sheaths is repeatedly emphasised in detail, in complete disregard of modern knowledge of the "closed" nature of the arachnoid demonstrated by such work as Weed's and Elman's. Lymphatics are freely supplied (in the text) to structures in which their presence has never been

demonstrated. Certain statements are not true of human structure—*e.g.* the description of a diverticulum of the third ventricle in the posterior lobe of the pituitary (p. 308 and fig. 427); the statement that the branches of the auriculo-ventricular bundle can be demonstrated by injection (p. 96); and the description of the blastocyst on p. 341.

The section on the central nervous system is the most unsatisfactory part of the book. Because of its inadequacy and occasional inaccuracy, it had much better have been omitted. The introductory description of the mid-brain, for example, reads: "The Mid-Brain connects with the medulla and cord. Several important nerves concerned with vision are connected to it. They pass through the crura cerebri, which consists of the tegmentum behind and the two bases pedunculi (crusta) in front." The only description of the function of the corpus striatum is an account of the effect of passing solutions of different temperatures through tubes applied to it. The drawings of sections of the brain stem are poor and there are several errors in labelling them.

A Manual of Surgical Anatomy. By LEWIS BEESLY, F.R.C.S. (Edin.) and T. B. JOHNSTON, M.B., Ch.B. (Humphrey Milford, Oxford University Press.) 4th edition. 1930. Pp. 563. 166 figs. 18*s.* net.

The appearance of yet another edition of "Beesly and Johnston" is an indication of success in its professed attempt to facilitate the study of surgical anatomy in the dissecting room and anatomical museum. If at times it reads rather like a manual of practical anatomy rewritten for the final year student, its method is yet justified, for the student is likely to acquire a better knowledge of the subject if led to retrace his steps along the pathway of his pre-clinical years than if he is presented with a collection of scattered items of applied anatomy which seems to have little relation to his earlier study. How much anatomical detail the senior student should retain will always be in dispute but, on the whole, the amount here given seems reasonable. Some rearrangement in places would keep the book truer to its own character.

On the surgical side a general criticism may be made of the description of operative procedures. These are usefully mentioned when they involve considerable applied anatomy, but there is a temptation to dilate on "anatomical" operations which are seldom actually performed—*e.g.* the opening up of the roof of the fourth ventricle. And there is the danger of giving an arbitrary selection to the exclusion of all mention of alternative standard procedures. Space could be saved and a charge of inequality avoided by the exclusion of matter encroaching on the province of the text-book of operative surgery.

The following detailed criticisms are in no wise meant to diminish appreciation of the book, which is, on the whole, the most useful one of its type which one has read. Lymph drainage is not always sufficiently described: the drainage of the appendix is not mentioned, and its relation to the association of diseases of the appendix, stomach, duodenum and gall bladder is therefore not brought home; the illustration of the lymph drainage of the breast (fig. 8) is unfortunate—the superficial plexus over the breast would appear to be limited by a definite peripheral lymph channel from which the largest group of efferents runs downwards and inwards over the costal margin! Some abnormalities of surgical importance are not mentioned—*e.g.* the occurrence of bipartite scaphoid in the hand and os Vesalianum in the foot, and the varieties of the cystic artery. The source of the vasomotor nerves on the arteries is given as entirely from the aortic plexus and hence the real anatomical reason for the conflicting results of periarterial sympathectomy (p. 128) is missed. The "Jackson's veil" described on p. 333 is certainly not the formation described by Jackson. The description of the action of the deltoid in raising the humerus (p. 8) should be revised. The rigid use of the B.N.A. and the frequent invocation of Stiles

and Kocher betoken the Edinburgh origin of the book (reference to the *foramina* of Monro is the less excusable). The said invocation is occasionally hardly fair, as in connection with the surface guide to the mastoid antrum, where the name of Macewen, if any, should be given.

Contributions from the Department of Anatomy of the Peking Union Medical College, Peking. Vol. v. *Collected Papers*, Nos. 84–114. 1930.

Prof. Davidson Black has incorporated in this volume thirty articles published in various journals by members of his staff. These papers relate to researches made during the last three years (1927–30). Research has been carried out in various branches of Biology as will be seen from the following classification of the contents of vol. v. Human palaeontology, seven papers, Prof. Davidson Black's own researches on Sinanthropus and on aeneolithic human remains being included in this group; eleven papers dealing with cytological problems, the chief contributor being Dr Wen-chao Ma; eight with zoological matters, Dr A. B. D. Fortuyn writing most of them. The remaining four papers are devoted to Human Anatomy and Anthropology. Altogether vol. v is one which the Director of the Anatomical Department of the Peking Union Medical College may well be proud of.

Warren's Handbook of Anatomy. Text by Robert M. Green, M.D., Assistant Professor of Applied Anatomy, Harvard Medical School. (Cambridge, Massachusetts: Harvard University Press; London: Humphrey Milford, Oxford University Press.) 1930. Pp. xiv + 384. 324 figs. 63*s.* net.

By the death of Dr John Warren in 1928 the Harvard Medical School was deprived of an able and devoted teacher of Human Anatomy and a strong and charming personality. For some years previous to his untimely death at the age of 54, Dr Warren had been engaged in the preparation of a topographical atlas of the human body. A very large number of dissections, many of them original in conception and admirably executed, had been made and many of the drawings had been completed. This material he bequeathed to the department which he had served so well, and his colleagues have undertaken its preparation for publication in his memory.

The book is well bound and beautifully printed on good paper, and it is clear that no expense has been spared in the effort to provide a worthy memorial. Despite the absence of colour, the illustrations are excellent, although those involving sections of bone are not convincing, and the exaggeration of the articular capsules as distinct entities in certain regions is artificial and somewhat misleading.

The Editor's task has been a difficult one, for it has fallen to him to supply most of the letterpress for a book which had already been begun by another hand. Difficulty has been experienced in determining what should be included and what should be excluded, and the final selection is not altogether satisfactory. Certainly much has been included which might well have been omitted, and one would be careful not to place the text in the hands of an uncritical student.

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THE INFLUENCE OF THE SYMPATHETIC ON THE PIGEON'S WING

By GREGOR T. POPA and FLORICA POPA
Institute of Anatomy, Jassy, Roumania

From the Institute of Anatomy, University College, London

The results described in our preliminary note to the Physiological Society (*Proc.*, Dec. 1928, *Journ. of Physiol.* vol. LXVII), in which we confirmed the effects of sympathectomy upon skeletal muscle described by John I. Hunter, have been questioned by A. E. Coates and O. W. Tiegs (*Australian Journ. of Exp. Biol. and Med. Sci.* vol. VII, 1930, p. 37) who suggest another explanation in these words:

> G. and F. Popa find that if, in the pigeon, from one to five sympathetic ganglia are severed from their attachments to the brachial nerves (C. 11–15) and then removed, there occurs a droop in the wing, thus confirming the conclusion of Hunter that the sympathetic nerves subserve plastic tone in the wing musculature. Hunter based his experiment on Langley's statement that the first thoracic nerve is the first by which preganglionic fibres emerge from the cord; so that severing the sympathetic chain immediately in front of this root should suffice to abolish all tone due to sympathetic action. We ourselves failed to obtain Hunter's effect. Meanwhile Popa states that "Langley's account of the sympathetic in birds ignores the presence of white rami communicantes (preganglionic fibres) above the 14th spinal nerves," thus depriving the bird's wing of the special anatomical peculiarity upon which Hunter relied for his demonstration. Hunter's own observation (if Popa's statement be correct) must therefore clearly be wrong. But it is only necessary to make a dissection of the pigeon's brachial plexus to realise that a droop in the wing following removal of the attached sympathetic ganglia cannot afford valid evidence to prove that sympathetic nerves play any direct part in maintaining muscular tone, for the ganglia are so firmly attached to the spinal nerves that it is quite impossible to remove them without doing injury to the adjacent spinal nerve fibres. . . . The sympathetic ganglion is so intimately associated with the main nerve trunk that its removal must inevitably produce injury to the latter. When it is remembered that there are five such ganglia, that they are about the size of a pin's head, and that they are comparatively inaccessible, it seems clear that injury to the brachial nerves, with consequent droop in the wing, could not possibly be avoided.

(*a*) In this passage Coates and Tiegs claim that our results are due to injury of the brachial nerves. We submit photographs of pigeons (Figs. 1, 2 and 3) operated upon by the method described in our note and quoted by Coates and Tiegs.

Fig. 1 shows a pigeon, distinguished in our note-book by the numbers 33–927. On 12 November, 1927, its left stellate ganglion was removed.

Figs. 2–3 show another pigeon (270–929) from which, on 10 October, 1929, the five left sympathetic ganglia of the brachial region were removed.

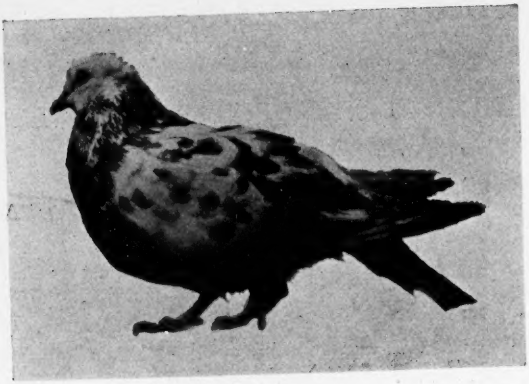
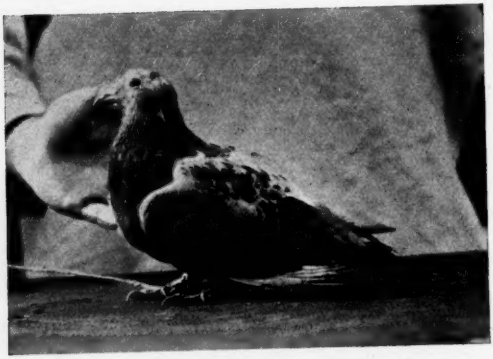


Fig. 1.



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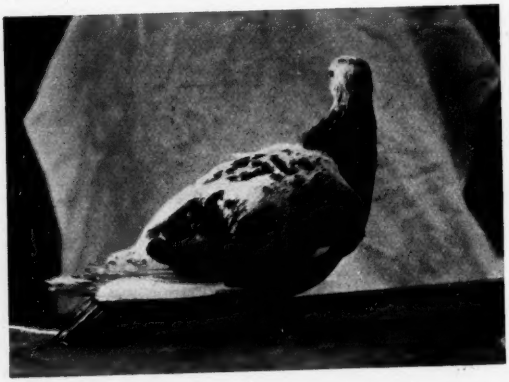


Fig. 3.

Both pigeons are still alive at University College, London. The photographs were taken in October, 1930, that is, in the case of pigeon 33–927, 35 months after the operation, and of pigeon 270–929, 12 months after.

The immediate effects described by Hunter still persist after all these months. Even when the animals walk about in their cage the wing on the operated side droops slightly. After an effort, however, the drooping becomes emphasised and is quite unmistakable. How can this be explained by the assumption of injury to the brachial nerves? Even if half the fibres had been cut they would be regenerated during the one and two years that elapsed in our experiments. As a matter of fact no brachial (somatic) fibres were cut. It might perhaps be argued that damage may have been inflicted on the nerve roots by pressure while lifting the roots. This eventuality we eliminated by purposely handling the brachial roots on the opposite side in the same way without, of course, actually removing the ganglia. No appreciable effect could be detected, however.

The relationship of the sympathetic ganglia to the brachial nerves is not so close as the criticisms suggest. These ganglia are surrounded by a connective tissue capsule and their enucleation is very easy. Pending the publication of our work *in extenso*, we may quote what we have written with reference to the method of removing ganglia:

> By using a fine hook the roots of the brachial plexus are gently lifted, the corresponding sympathetic ganglia are displayed and with a fine ophthalmic knife the ganglia can be separated without any direct damage to the spinal nerves. After separation the sympathetic chain is pulled out gently and cut with scissors at both ends.

(*b*) The existence of preganglionic fibres above the limit described by Langley is fully demonstrated in our work. Langley states that "the last large nerve to the brachial plexus, i.e. the last cervical nerve, is the first to cause the movements of feathers and other effects of cervical sympathetic stimulation."

The last cervical nerve is the 14th spinal nerve in the pigeon and according to Langley, above this level no nerve fibres from the spinal cord pass to the sympathetic ganglia.

Here we present two pictures of brachial nerves and of corresponding sympathetic ganglia together with their reciprocal relations.

Fig. 4 shows the 13th spinal nerve, one segment above the upper limit of the sympathetic origin as described by Langley. A large contribution of preganglionic fibres (*Pr.*) is made to the corresponding sympathetic ganglion by the somatic nerve (its motor root) and from this sympathetic ganglion a large bundle of fibres (postganglionic fibres (*Po.*)) joins the somatic nerve.

Fig. 5 shows the 12th spinal nerve, two segments above the upper limit described by Langley for the origin of the sympathetic. One can see preganglionic fibres (*Pr.*) coming from the motor root of this nerve to the corresponding sympathetic ganglion. These fibres scatter in the ganglion and some of the postganglionic fibres (*Po.*), originating in the same ganglion, are seen joining the somatic fibres of the same spinal nerve.

(*c*) How the positive results of Hunter, which we confirm, agree with this finding of unknown preganglionic fibres is explained largely in our paper (which is not yet published). We quote again a paragraph of this lengthy manuscript:

> The numerous results reported so frequently in the literature by different observers are due to their adherence to Langley's descriptions and diagram. The white rami have been cut below the level of the 14th spinal nerve only, the larger part of the sympathetic innervation to the skeletal muscles of the left wing has been left intact. It is not surprising therefore that positive results were not obtained constantly. Hunter himself was guided in his experiments by Langley's statement, but he soon observed that the results were more certain if the sympathetic trunk is cut between 13th and 14th spinal nerves. "*In sea gulls I invariably cut the dorsal and ventral trunks immediately behind, or below, the penultimate* (13*th*) *cervical nerve as well*[1]."

In the very place where Hunter cut the sympathetic chain we have found that the sympathetic trunk is really *a ganglion*. Instead of a simple internodal ramus, consisting only of nerve fibres, there is in the pigeon a long ganglion containing nerve cells which extend in between the nerve roots.

Fig. 6 shows exactly the interganglionic communication of the sympathetic chain between the 13th and 14th brachial nerves, the place where Hunter performed the majority of his experiments.

Eventually Hunter, operating on this most important contribution of the sympathetic to the innervation of the skeletal muscles of the wing, obtained almost constant positive results.

[1] John I. Hunter: Lectures on the sympathetic innervation of striated muscle. Delivered by Professor Elliot Smith at University College, London, 1925, p. 33.

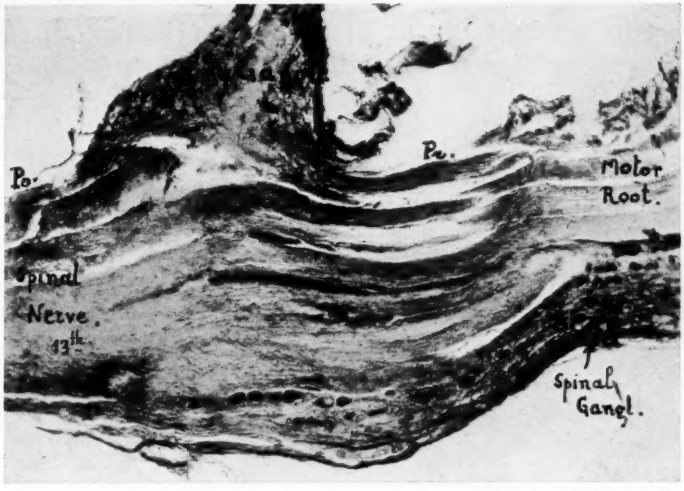


Fig. 4.

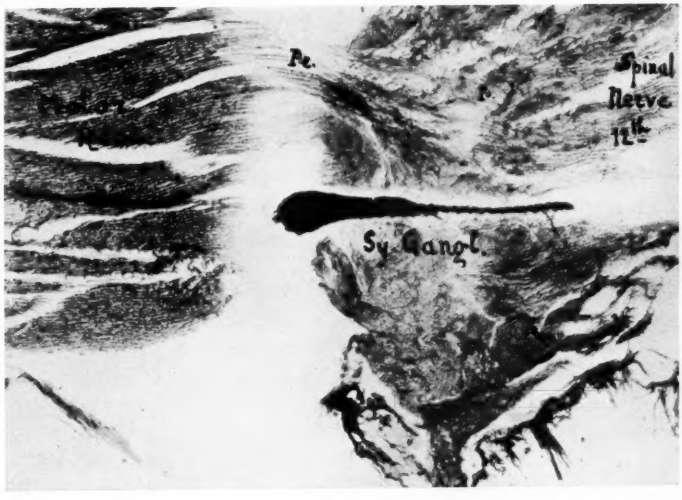


Fig. 5.

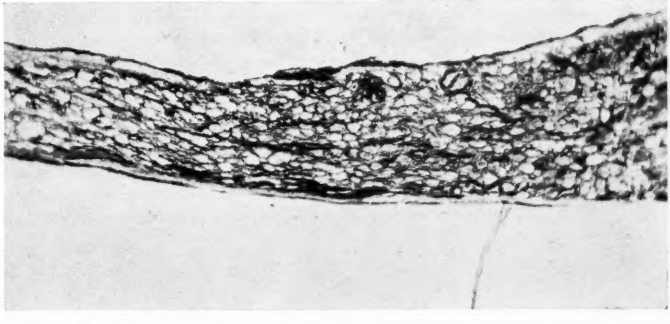


Fig. 6.

THE EARLY DEVELOPMENT OF THE FERRET: THE CYTOPLASM

By DONALD MAINLAND
Professor of Anatomy, Dalhousie University, Halifax, Canada

INTRODUCTION

One of the most fundamental problems of embryology is the structure of the unsegmented ovum, and yet, compared with the widespread interest displayed in the cytoplasm of non-mammalian ova, the attention paid to this aspect of mammalian ova has been very limited. It has been left almost entirely to the Belgian school of the Van der Strichts to carry on minute investigation of mammalian ooplasm, to emphasise its importance and to disclose the fact that each mammalian species has its characteristic ovum. It appears to be felt by some investigators that the cytoplasm of the mammalian ovum is outside the province of the embryologist, although why he should avoid cytology in this way, while investigating so thoroughly the nuclear structure of the ovum, is hard to understand. The one aspect is assuredly as important as the other, and it is on this account that the author presents these records of investigations carried out on the cytoplasm of the unsegmented tubal ovum of the ferret.

MATERIAL AND METHODS

There are three main types of treatment that may be used to disclose the structure of the ooplasm. The first is the common method, whereby, after fixation in, for example, formol, Zenker's or Perenyi's fluids, the ovum is carried through fat-solvents, e.g. xylol, into paraffin. By this method the lipoid material is not shown, nor are the mitochondria well displayed. The second type of method—fixation in a fluid containing osmic acid—enables one to preserve the lipoids that contain unsaturated fatty acids. The third type of method—employment of a special mitochondrial technique—may be combined with the second type just mentioned, but the treatment by Flemming's fluid, unless the acetic acid in it is very small in amount, does not preserve the mitochondria (Lee, 1928, p. 332).

The specimens investigated in the present study had not been treated by the third type of method, but some had been subjected to the first type and others to the second. The ova were the same as those used in a recent investigation of the pronuclei (Mainland, 1930)[1], being 101 ova liberated from 30 different

[1] The work referred to (Mainland, 1930) was a quantitative study of the structure of ferret pronuclei. Attention was paid in it to such matters as staining, position and relative size of chromatin particles, wrinkling of pronuclear membrane, fineness of reticulum; an endeavour being made to correlate all changes with the development of the pronuclei. Thus, nonbasiphilic globules were found only in pronuclei after they had left the periphery of the ovum. Statistical tests were applied to the data, and it was shown that when such precautions were taken it was not possible to describe an ordered series of transformations as has been done for the pronuclei of some other Mammals.

The influence of technique of preparation received special attention, e.g. Perenyi's fixative was shown to produce large particles of chromatin more commonly than did the other fixatives.

Descriptions were given of an ovum with a sperm tail in it and of a trinucleated ovum.

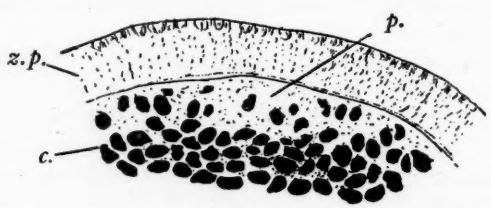
ovaries belonging to 19 different animals. All the ova were at stages of development found immediately after ovulation. Seventy-one out of the 101 were at the pronuclear stage; some were at the second polar spindle stage; and some at the stage of the first segmentation spindle. Paraffin sections cut at 10 μ were used throughout. For further details regarding the preparation, reference should be made to the article mentioned above (Mainland, 1930, p. 262).

As in the study of the pronuclei, statistical methods were applied to the data, for it is only by such tests that assurance can be obtained that one's statements are not based merely upon personal opinion, and that one's opinion is not formed upon inadequate data. In reading reports of many careful embryological investigations, the author realises how much greater would be his feeling of conviction if only the data had been subjected to some simple quantitative tests, or at least set forth in such a way as to make these tests possible. The statistical test chiefly used here is the Chi Square test, discussed and exemplified in the paper already mentioned (Mainland, *l.c.*, p. 263). The probable error method, and the regression method are also used. At the appropriate place in the description the purpose and nature of the tests are indicated. At this point reference should be made to the frequent use of the term "significant." When this word is applied, for example, to a difference between quantities, it means that the odds are about 20 (or more) to 1 that the difference is not accidental or due to "chance." Similarly, if an association between two phenomena is said to be "significant," the meaning is that the odds are at least 20 to 1 in favour of such an association.

STRUCTURE OF OVUM

Histological appearance

The fundamental structure of the cytoplasm of the tubal ovum of the ferret has been indicated by Robinson (1925). The cytoplasm consists chiefly of



Text-fig. 1. A portion of a Flemming-fixed ovum, showing dark, lipoid-bearing "yolk bodies." (Specimen merely tinted with eosin; camera lucida drawing; magnification approx. 1150.) *c.*, edge of central portion; *p.*, peripheral portion, containing less lipoid than central portion; *z.p.*, zona pellucida.

lipoid[1]-bearing material commonly called yolk or deutoplasm, which appears as black globules in the ova fixed in Flemming's fluid (text-fig. 1 and Pl. II).

[1] The term "lipoid" is used in this article in its widest sense, to signify a fat or fat-like body.

After fixation in Zenker's or Perenyi's fluid the lipoid is dissolved out during the processes of dehydration and clearing. The result of such processes is shown in all the figures of Pl. I, where the cytoplasm presents a mass of vacuole-like spaces, the mass being surrounded by a comparatively narrow granular zone. This granular zone here and there also contains in the Flemming-fixed ova some lipoid globules (text-fig. 1).

Comparative histology

As mentioned above, the importance of the structural differences between the ova of different Mammals has been emphasised chiefly by O. van der Stricht (1923, etc.) and his collaborators. Of the ova illustrated by O. van der Stricht (*l.c.*) the one most closely resembling the ferret in respect of lipoid material is that of the dog. The pig contains even more such material (Corner, 1928, p. 1121). The ova of the cat (R. van der Stricht, 1911; see also Hill and Tribe, 1924) vary in respect of the amount of lipoid. Some contain almost as much lipoid as do those of the ferret, while others contain less. Corner (*l.c.*) makes the interesting suggestion that the greater abundance of yolk in the ova of these animals as compared with those of the rat, guinea-pig and rabbit is correlated with the extent to which the ova are developed before they are attached to the uterus. One of the most serious objections to this suggestion is furnished by the ova of the cat. These, as has been mentioned, can be divided into two classes according to the amount of lipoid they contain. If Corner's theory is correct it would apparently be necessary to suppose that these two classes of ova became embedded in the uterus at different times. There seems to be no evidence of this. Further light is thrown on the theory by consideration of other animals. Summaries of information on the implantation of Mammals are to be found in Robinson (1904) and in Marshall (1922). The ova of the dog, cat, pig and also of the ferret are more advanced before implantation than those of, for example, the mouse, in which the lipoid of the ovum is very scanty compared with that of the other animals just mentioned. The ovum of the guinea-pig, however, may contain relatively as much lipoid as that of the cat (compare Pl. XV, fig. 40 of R. van der Stricht, 1911 with Pl. XII, fig. 93 of O. van der Stricht, 1923), and yet the guinea-pig ovum becomes implanted at an earlier stage than that of the cat (Marshall, 1922, pp. 472 and 444). Thus Corner's suggestion appears open to serious criticism.

Chemical structure

The evidence of the chemical nature of the yolk-bodies is obtained solely from the action of osmic acid in Flemming's fixative. The present state of knowledge of osmic fixation of fats is summarised by Parat (1927). Osmic acid is a specific reagent for unsaturated fatty acids, and practically the only interesting member of these in the animal organism is oleic acid.

On comparison of the Flemming-fixed ova with those fixed in Zenker or Perenyi, it is seen that the vacuoles in the latter specimens correspond to

the darkly stained lipoid globules of the former. This seems to suggest that the two elements in the cytoplasm are (*a*) the protoplasmic framework and (*b*) the lipoid, containing unsaturated fatty acid radicles, this lipoid being dissolved out after the non-osmic fixatives.

The blackening with osmic acid is very intense, and the question naturally arises whether the original lipoid contains only unsaturated fatty acids or whether part of it contains saturated fatty acids, and is therefore not preserved by osmic fixation. Analogies with non-mammalian ova are of course dangerous, but it is of interest to note, for example, that two of the lipoids in egg-yolk are lecithin and sphingomyelin. Of these the former contains unsaturated as well as saturated acid radicles (Maclean and Maclean, 1927, p. 26), and the lignoceric acid radicle present in sphingomyelin (*ibid.* p. 62) is a saturated acid (Leathes and Raper, 1925, p. 13). As is well known, the ordinary fats occur naturally as mixtures of saturated and unsaturated fats. One would therefore expect that the lipoids of the ferret ovum contained saturated as well as unsaturated fatty acid radicles, and one must harmonise that view with the fact that the blackening of the globules is intense, as if they were entirely composed of lipoids with unsaturated fatty acids. From the work summarised by Parat (1927), it appears that, when less than 50 per cent. unsaturated acid is present, the blackened material is very soluble, but, when more than 50 per cent. unsaturated acid is present, it is very stable after fixation by osmic acid. Since, therefore, the globules in these ferret ova persisted after being subjected to powerful fat solvents, one may conclude that the fatty material contained at least 50 per cent. of the unsaturated fatty acid. It should be observed that these statements imply that a considerable amount of saturated fatty acid might be present and yet the lipoid globules might be very darkly stained. It is conceivable that the particles containing the unsaturated fatty acid radicles are intimately mixed up with particles containing saturated fatty acid radicles. When the lipoid containing the saturated acids was dissolved out, the unsaturated acids, already made insoluble by the osmic acid, would remain and the blackened material would be so uniformly distributed as to give a very dark appearance. It may be remarked in passing that there is still a field open for carefully controlled histological experiments to determine the results of osmic acid fixation of various artificially prepared emulsions of different lipoids.

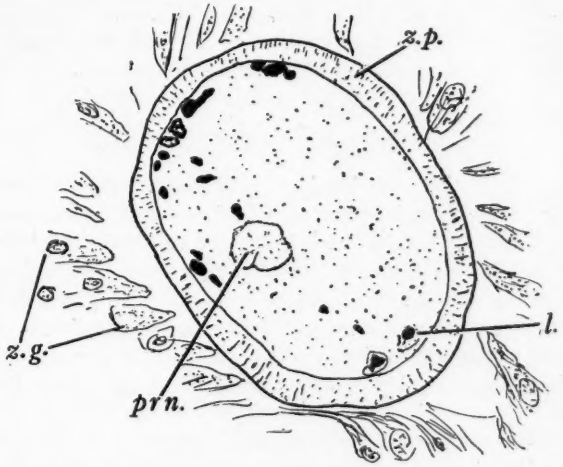
Minute structure of yolk globules

The question that next arises is whether the globule is a simple droplet or has a framework of protein or other material. When fixed in Zenker's or Perenyi's fluid and stained by Heidenhain's iron-haematoxylin and faintly tinted by eosin, the network between the vacuoles is grey or blue-black, and the vacuoles may be almost colourless. When fairly heavily stained with eosin the vacuoles take on a pink tinge. It may be asked whether this does not indicate some material, probably protein, in the vacuole. The size of the globule or vacuole affords the solution of this problem. As may be estimated

from fig. 4 of Plate I, the vacuole is in the neighbourhood of 3 μ in diameter. The sections were cut at 10 μ, and the globules, as shown in the figure, are usually much less than 3 μ from their neighbours (see also text-fig. 1). Hence, in a section, the walls of two or even three globules intervene between the source of light and the eye, and the vacuolar appearance is due to the thinness of these interglobular walls, not to the absence of material. The pink tinge can therefore be explained as a stain of the interglobular material and does not indicate a framework in the globules.

Abnormal ova

Although the typical tubal ovum, like the typical large ovarian ovum, shows abundant lipoid, four ova were examined in which, after fixation in



Text-fig. 2. An abnormal ovum (no. 76), fixed in Flemming, but showing very little lipoid. (Specimen merely tinted with eosin; camera lucida drawing; magnification approx. 500.) *l.*, lipoid globule; *prn.*, pronucleus; *z.g.*, zona granulosa; *z.p.*, zona pellucida.

Flemming's fluid, the lipoid globules were almost entirely absent (e.g. text-fig. 2). These ova appear to merit some detailed discussion, to ascertain what light they throw on the technique of preparation and on the abnormal metabolism of ova. All of these ova were at the stage of central or subcentral pronuclei. Three were from the left uterine tube of one animal, and the same tube showed two other ova in which the lipoid substance was abundant. Hence the absence of lipoid was not due to a characteristic of one ovary. These two sets of ova from the same animal—one set with abundant lipoid and the other with practically none—were on different slides, and therefore differences in the technique might be responsible. The lipoid from the one set might have been removed during preparation, owing to their being subjected

to more intense solvent action. Such an argument could not, however, apply to the other ovum (no. 76), where the large ovarian ova, present in the same sections, and therefore subjected to the same treatment, contained the usual amount of lipoid material. This abnormal ovum (text-fig. 2) was a fertilised ovum apparently held back mechanically in the periovarian space by a cyst-like body, the nature of which could not be determined. The other three ova were all in the uterine tube and there was no evidence of mechanical hindrance to development. One may therefore legitimately look on ovum no. 76 as degenerate, although it is unprofitable to speculate on the cause of degeneration. It is more valuable to compare the appearance of this degenerate ovum with that of degenerate ovarian ova. In the latter, degeneration is denoted by the presence of large masses of osmic-blackened fatty material, whereas in this fertilised ovum the lipoid has almost entirely disappeared, that is, the unsaturated fatty acids have been saturated and so have escaped fixation by the osmic acid. Either the degeneration is of a different type from that of ovarian ova, or the phenomena proceed at a different rate.

POLARITY OF THE CYTOPLASM

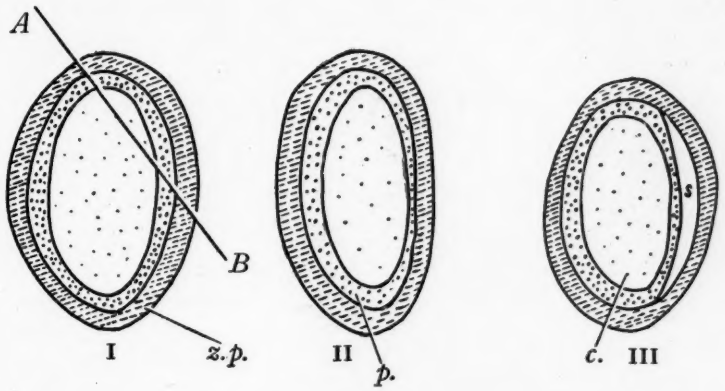
The most distinctive contribution made by O. van der Stricht and his collaborators to the knowledge of mammalian ova is the demonstration of cytoplasmic polarity, that is, the existence of two poles, an "animal" pole marked by granular protoplasm, and, opposite to this, a "vegetative" pole marked by greater abundance of yolk or lipoid material. The article by O. van der Stricht (1923) contains not merely a summary of the discoveries made by himself and his collaborators, but a detailed account of the cytoplasmic transformation in the mammalian ova studied by them, and also a large number of illustrations. The original reports on which that record was based may be found chiefly in such works as those of Lams (1913) on the guinea-pig, Lams and Doorme (1908) on the white mouse and guinea-pig, O. van der Stricht (1905) on the bat, and R. van der Stricht (1911) on the cat. From this body of work a polar arrangement of the ooplasm has been established as occurring in the bat, white mouse, guinea-pig and cat. With regard to the dog the chief information is contributed by O. van der Stricht in the article already mentioned (1923). Polarity is stated to be found in this animal, but a critical examination of the illustrations given there does not convince the present author of its presence in the tubal ova at the pronuclear stage.

Sources of error

In the ferret, owing to the large amount of lipoid material, it is not immediately easy to recognise a polar distribution of deutoplasm. When polarity appears to exist, therefore, one must eliminate all possible sources of error. In the investigation here recorded the sources of error considered were as follows:

(1) Position of section through ovum. Thus, in text-fig. 3 I, the breadth of the outer granular zone near the end *A* of the line *AB* would be less than near the end *B*. This error can be eliminated by careful focusing and by comparison with the breadth of the zona pellucida adjacent.

(2) Mode of cutting of ovum. The part first met by the microtome knife might be crushed, so that the size of the granular zone on two sides of the section might be artificially different (text-fig. 3 II and III). This source of error can be eliminated by observing whether the zona pellucida adjacent is flattened or whether the perivitelline space (*s* in text-fig. 3 III) between the ovum and the zona pellucida has been enlarged.



Text-fig. 3. Diagrams of ova. In I, the peripheral granular zone (closely dotted) is fairly uniform in thickness, and in the section of the drawing no polarity of the cytoplasm would appear. If the section were cut along the line *AB* the one part would show a broader granular area than the other. In II, the ovum has been flattened on the right, and the granular zone is narrower than on the left. In III, the ovum has been knocked away from the zona pellucida, and the granular zone is again artificially narrowed. *c.*, central portion, sparsely dotted, lipoid-bearing; *p.*, peripheral portion, closely dotted, granular; *s.*, perivitelline space; *z.p.*, zona pellucida.

(3) Fixation. Most of the ova were fixed in the uterine tube, one aspect of which faces the ovary and the other the abdominal cavity. It was possible that the fixing fluids reached one side of the ova earlier than the opposite side or in a different concentration. Allowance was made for this error, but it is improbable that it was important in the case of such a small body lying free in the uterine tube.

Ova in which polarity was demonstrated

After these sources of error had been eliminated it was found that out of 100 of the ova examined the proportion of ova classified according to polarity were:

Ova with definite polarity	29
Ova with possible polarity	21
Ova without polarity	50
	100

Illustrations of ova with polarity are shown in Pl. I.

It should be noted[1] that in the discussion that follows the terms "animal" and "vegetative" poles are usually avoided, because they appear to imply that the polarity here found corresponds to the polarity of non-mammalian ova, an assumption that is not immediately obvious.

Reasons for lack of polarity

To account for the ova in which no polarity was found various tests were applied. The ova fixed in Perenyi's fluid were compared with those fixed in Zenker's fluid, only those ova that were stained by Heidenhain's iron-haematoxylin being considered. The Chi Square test showed no association between these fixatives and the presence or absence of polarity.

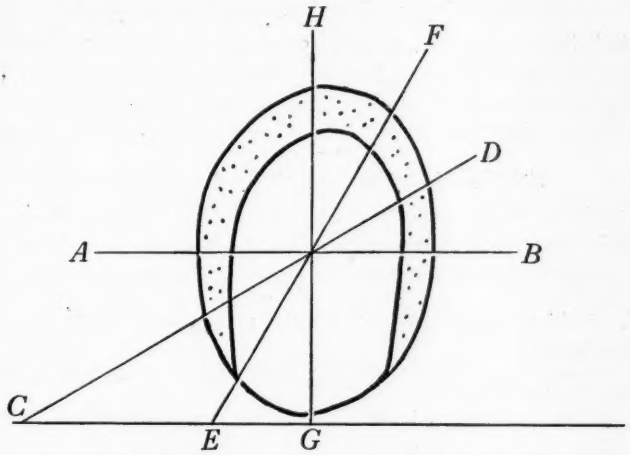
Out of 16 ova fixed in Flemming's fluid none showed definite polarity. Allowance was made for the 4 ova mentioned above in which almost all of the lipoid had been removed, and then the others were added to the Zenker- and Perenyi-fixed ova just considered. The Chi Square test then showed a high association between fixative and polarity, an association due to the introduction of the Flemming-fixed specimens. Most of these Flemming-fixed ova had been merely tinted with eosin and not stained further. Fixation in Flemming's fluid, therefore, without staining, does not clearly demonstrate polarity.

Among the ova fixed in Zenker's fluid a comparison was made between those stained by Heidenhain's iron-haematoxylin and eosin and those stained by Mayer's haemalum and eosin. The Chi Square test showed that there was a definite association between staining and the demonstration of polarity. None of the 14 ova stained by Mayer's haemalum and eosin showed definite polarity, while 13 out of 23 stained by Heidenhain's iron-haematoxylin and eosin showed definite polarity.

Since Zenker and Perenyi fixation do not differ essentially in regard to the demonstration of polarity, it may be asked why, when the staining is the same, some of the ova fixed by these methods show polarity and others do not. The explanation appears to depend upon the plane of section of the ova. Let it be assumed that every ovum has a polarity similar to the ova in fig. 1 or fig. 2 of Pl. I. It is reasonable to suppose that there are equal

[1] The lipoid pole is not devoid of granular material, nor is the granular pole devoid of lipoid.

chances for an ovum to be cut in any plane with reference to the interpolar axis. Text-fig. 4 represents an ovum with a peripheral granular region and two poles, granular and lipoidal. For simplicity only those sections passing through the centre of the ovum will be considered. Some sections will pass horizontally through the centre (plane *AB*), and in such sections no polarity will be detectable. Some will pass at an angle of 30° to the horizontal (plane *CD*), and then the polarity may not be definite, although actually the granular regions may not be of equal extent at the two ends of the section. The definiteness in this case depends on the exact plane of the section and the exact extent to which the granular matter encroaches on the lipoidal pole. Other sections will pass at an angle of 60° to the horizontal (plane *EF*), and so will demonstrate



Text-fig. 4. Diagram of ovum, showing the different effects of cutting along different planes. The granular zone is dotted. (For description see text.)

polarity. Others again will pass at right angles to the horizontal (plane *GH*), and then also the sections will show definite polarity. Any other planes might be chosen, but those selected are representative and are arranged at equal distances from each other. It should also be noticed that these planes (except *GH*) all commence to the left of *G*, and there will be as many planes commencing to its right. It is, however, sufficient to consider only the one set. On an average, therefore, out of every 4 sections there will be 2 showing polarity, 1 showing doubtful polarity and 1 not showing polarity. The comparison with the actual numbers is shown in Table I. The actual numbers agree very closely indeed with the theoretical. Hence the apparent absence of polarity can be very well accounted for by the plane at which the sections of the ova were cut.

Table I. *Comparison between the actual numbers of ova classified according to polarity and those expected according to the differences in planes of section. (The ova concerned are those fixed in Zenker or Perenyi and stained with Heidenhain's iron-haematoxylin.)*

No. of ova	Polarity definite	Polarity doubtful	Polarity absent	Total
Actual (a) ...	27	10	14	51
Theoretical (t) ...	25·5	12·75	12·75	51
$a-t$	1·5	−2·75	1·25	0
$\frac{(a-t)^2}{t}$	0·09	0·59	0·12	0·80

$\chi^2 = 0{\cdot}80$; $n = 2$; P is between 0·90 and 0·80.

Relationship of nuclear development and polarity

The Chi Square test showed that there was no association between the stage of development of the nuclear material and the presence or absence of cytoplasmic polarity, that is, there was no distinguishable loss or gain of polarity during migration of the pronuclei to the centre of the ovum.

Relationship between polarity and polar bodies

The position of the polar body in relation to the granular pole was expressed in terms of the hours of the clock, 12 o'clock being at the centre of the granular pole. Table II shows the number of polar bodies found at the

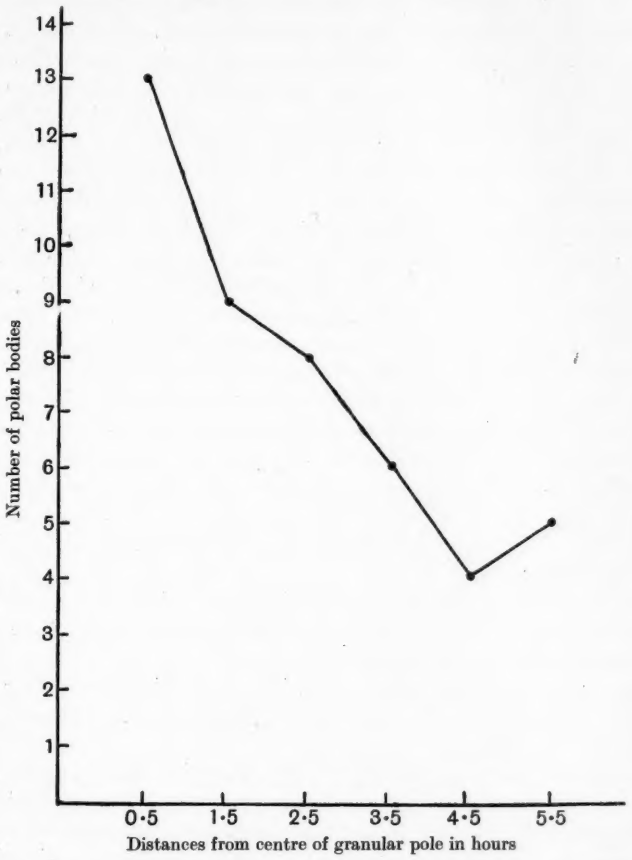
Table II. *Position of polar bodies in relation to centre of granular pole of ovum*

Distance in hours from granular pole	0–1·0	1·1–2·0	2·1–3·0	3·1–4·0	4·1–5·0	5·1–6·0
Number of polar bodies	13	9	8	6	4	5

different distances up to six hours from the centre of the granular pole. The coefficient of correlation between the distance from the centre of the granular pole and the number of polar bodies found is −0·931. There is therefore a very high negative correlation, that is, the farther away one goes from the centre of the granular pole, the fewer polar bodies one meets. To show whether this coefficient was significant or due to chance, Fisher's t-test was applied (Fisher, 1930, p. 159). $t = 15{\cdot}7$; $n = 4$, and therefore the coefficient of correlation was highly significant.

The graph in text-fig. 5 shows how closely the numbers correspond to a straight line. The straight line most closely fitting the actual numbers is expressed by the equation $Y = 12{\cdot}386 - 1{\cdot}629x$, where Y is the number of polar bodies calculated from the equation, and x is the number of hours from the centre of the granular pole. This equation is the regression equation of y (the number of polar bodies) on x (the number of hours), and by use of it one can predict very closely the number of polar bodies found at the various distances from the granular pole.

The fact that most polar bodies are found near the granular pole suggests that this pole is probably the "animal" pole, that is the one at which the polar divisions occur. The reason for the almost rectilinear fall in frequency is not immediately evident, for it would be expected that most of the polar bodies should be near the "animal" pole, and that there would be a more sharp fall in numbers as one passed from the "animal" pole.



Text-fig. 5. Graph showing numbers of polar bodies found at different distances from the centre of the granular pole. Distances are in "hours."

In the interpretation of this phenomenon it is important to recall the experimental work on the frog's ovum referred to by Wilson (1925, p. 1021). This work showed that if the ovum be kept inverted the cytoplasmic materials undergo a rearrangement under the influence of gravity. This might be suggested as the cause of the peculiar arrangement of polar bodies with reference

to the poles in ferret ova, but it is obvious that it could not wholly account for the phenomena, since there would be roughly equal chances of the ova being inverted, lying on their sides, or being correctly orientated at the time of fixation, and therefore the polar bodies should be distributed at random with reference to the poles. This is not the case.

A possible explanation of the distribution of the polar bodies is the "reversal of polarity," stated by O. van der Stricht and his collaborators to occur in the bat and guinea-pig, but not in the white mouse, dog or cat (O. van der Stricht, 1923). This reversal is a displacement of the deutoplasm (fat globules, etc.) soon after fertilisation, towards the opposite pole, so that the original "animal" pole becomes the "vegetative" pole. Examination of the figures given to illustrate this in O. van der Stricht's article already referred to, reveals the fact that the polar bodies are only rarely attached to the ovum at this stage of development, and therefore one is justified in doubting whether the polar bodies are in their original position. There is, however, one fact that might support the suggestion that the change in position is due to a change in structure of the ovum, and not in the position of the polar bodies. This fact is that the two polar bodies in the illustrations mentioned, even although not attached to the ovum, are close together, and it might be claimed that the polar bodies are not likely to migrate together. If this argument holds, then the opinion that reversal of polarity occurs in the guinea-pig can be substantiated, for the Chi Square test, applied to O. van der Stricht's illustrations, showed a significantly greater proportion of ova with polar bodies at the "vegetative" pole when the pronuclei were central than before that stage.

To determine whether in the ferret the position of the polar bodies varied with the stage of development of the pronuclei, the ova were divided into two classes as follows:

Class A: At stage of second polar spindle or peripheral pronuclei. Mean distance in "hours" between the polar body and the centre of the granular zone 2·161; probable error ± 0·25.

Class B: At stage beyond class A, i.e. pronuclei subcentral or central. Mean distance as above 2·767; probable error ± 0·24. Difference 0·606; probable error ± 0·35.

The difference, being less than three times its probable error, is not significant. The result does not agree with the theory of reversal of polarity. The original granular zone has, presumably, remained granular, and the distribution of the polar bodies is best explained as due to their migration, for, if the polar bodies migrate, there will naturally be fewer and fewer the farther one passes from the "animal" pole. The cause of the migration is obscure.

Relationship of polar axis to pronuclei

In the mammalian ova observed by O. van der Stricht and his collaborators there was detected a general law that, when the pronuclei were centrally placed in the ovum, the line between the centres of the pronuclei passed through

the two poles. In the ferret ova an estimate was made by the eye of the angle between the internuclear plane and the polar axis. In 12 ova the plane was at right angles to the axis, in 9 ova at about 45° to the axis, and in 5 ova it was parallel to the axis. This suggests agreement with the law just stated, but statistically these numbers were shown not to be significant.

Relationship of polar axis to plane of first segmentation

There was only one ovum in which an indication of this could be determined. In this ovum the polar axis lay in the equatorial plane of the first segmentation spindle. If no change in the position of the spindle occurred, the ovum would divide so that the first two blastomeres would be similar in respect of the granular and lipoid material.

BASIPHIL GRANULES

It has been mentioned above that the technique employed in the preparation of these specimens did not demonstrate mitochondria. It was noted, however, that many of the ova displayed small granules[1] that took on the stain of the basic dye (Pl. I, fig. 3). They were of about the size of the smallest chromatin granules of the pronuclei. The chief interest of these bodies lies in connection with Kremer's statement (1924) that there is in the mouse elimination of chromatin from the pronuclei with the resulting formation of chromidial substance in the ooplasm. Some of the ferret ova suggested a confirmation of this opinion, but more exact investigations were undertaken to prove or disprove it.

Association with technique

When Heidenhain's iron-haematoxylin was used, the Chi Square test showed that the presence or absence of the basiphil granules was independent of fixation, the fixatives being Zenker, Perenyi and Mann with formol. Out of 57 ova so fixed and stained, 44 contained definite basiphil granules. The Flemming-fixed ova were unsuitable for demonstration of these particles, because of the numerous black lipoidal masses.

Out of 14 ova fixed in Zenker's fluid and stained by Mayer's haemalum and eosin, none showed definite basiphil granules; whereas out of 24 Zenker-fixed ova, stained with Heidenhain's iron-haematoxylin, 17 showed basiphil granules. The Chi Square test showed that this association was highly significant.

Among the specimens stained by Heidenhain's iron-haematoxylin it appeared possible that the deeper stained ova were more liable to contain basiphil granules, but the Chi Square test showed no association between depth of staining and presence of these granules.

[1] In the cytoplasm of some of the ova bodies were met that were associated with similar bodies in the zona pellucida. A separate communication dealing with these is in preparation, and further mention of them has no bearing on the present investigations.

Association with pronuclei

If the basiphil granules were due to elimination of chromatin, it would be expected that such granules would be present in the ova with central pronuclei more frequently than in the ova with non-central pronuclei. The Chi Square test showed that this was not so.

It may be recalled (Mainland, 1930) that some of the central pronuclei showed non-basiphil globules—colourless or eosin-stained. If the basiphil granules in the cytoplasm were products of chromatin elimination, it was reasonable to suppose that they would be more frequently met in the ova of which the pronuclei showed non-basiphil globules. The Chi Square test demonstrated that this was not so.

Finally, if the basiphil granules were derived from the pronuclei, it would be expected that there would be a preponderance of ova in which the granules were near the pronuclei. The Chi Square test showed, however, that far more ova had granules scattered in the cytoplasm than had them near the pronuclei.

There is, therefore, no reason whatever to suggest that these basiphil granules were in any way derived from the pronuclei. The necessary conclusion is that they are cytoplasmic. There is nothing to indicate that they are products of the imperfect fixation or breakdown of mitochondria, and therefore their origin and function is still undetermined.

ACKNOWLEDGMENTS

I wish again to record my indebtedness to Prof. Arthur Robinson for the loan of the specimens on which these observations were made, and to the trustees of the Moray Fund of the University of Edinburgh for financial assistance in the preparation of some of the specimens.

The major part of the investigation was carried on in the Department of Anatomy of the University of Manitoba, and my thanks are specially due to Dr C. H. Goulden, of the Agricultural College of that University, for help in the statistical work, and to Miss Nason, of the Department of Pathology, for the preparation of the photographs.

SUMMARY

Serial paraffin sections, 10 μ thick, of 101 ova of the ferret were examined, from 30 different ovaries and 19 different animals. All were at the stages between ovulation and completion of the first segmentation. The types of fixative employed were (*a*) those that did not preserve lipoid, and (*b*) osmic acid for preservation of lipoid. Special mitochondrial technique was not used. Statistical analysis was applied to the data.

The cytoplasm consists chiefly of a mass of lipoid-bearing material, this mass being surrounded by a granular zone with little lipoid. It appeared very doubtful if (as Corner suggested) the different amounts of lipoid material

in different mammalian ova are associated with the stage of development of the zygote when it is implanted in the uterus (p. 413).

The effect of osmic acid shows that the lipoid contains at least 50 per cent. unsaturated fatty acid. Arguments are adduced to suggest that saturated fatty acid radicles are also present (p. 414).

There is no evidence in favour of the suggestion that a protein framework exists in the lipoid globules (p. 415).

Four abnormal ova are discussed (p. 415), in which lipoid was almost entirely absent. One of these was definitely degenerate, and therefore this degeneration differs markedly from that of large ovarian ova, in which masses of osmic-blackened lipoid are present.

After various sources of observational error had been eliminated (p. 417), definite polarity of the cytoplasm was established in 29 out of 100 ova. Fixation in Zenker's and Perenyi's fluids demonstrated polarity equally well. Fixation in Flemming's fluid, without staining, did not demonstrate it clearly. Staining by Mayer's haemalum did not demonstrate it well, compared with staining by Heidenhain's iron-haematoxylin.

The apparent lack of polarity in some Zenker- or Perenyi-fixed specimens stained by Heidenhain's iron-haematoxylin can be accounted for by the plane of section of the ovum (p. 419).

There was no appreciable loss or gain of polarity during migration of the pronuclei to the centre of the ovum.

The numbers of polar bodies found varied inversely as their distance from the centre of the granular pole, and the relationship was expressed by a rectilinear regression equation. This suggests that the granular pole was in reality the "animal" pole and the lipoidal pole was in reality the "vegetative" pole. The arrangement of polar bodies is explained, not by the reversal of polarity due to moving of the deutoplasm, but probably by migration of the polar bodies.

The relationship of the cytoplasmic polar axis to the central pronuclei and to the first segmentation spindle was investigated (pp. 422–23).

Fine basiphil granules were met in the cytoplasm of some of the ova. The occurrence of these was independent of the fixatives (Zenker, Perenyi or Mann with formol). The granules were demonstrated by Heidenhain's iron-haematoxylin and eosin but not by Mayer's haemalum and eosin.

It has been shown (p. 424) that there is no reason to suggest that these granules are derived from the pronuclei. They are cytoplasmic, but their origin and function is undetermined.

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DESCRIPTION OF PLATES I AND II

(All the illustrations are photographs of ferret ova.)

PLATE I

Fig. 1. An ovum showing polarity. Fixed in Perenyi's fluid; stained by Heidenhain's iron-haematoxylin. Magnification 300.

Fig. 2. An ovum showing polarity. Fixed in Zenker's fluid; stained by Heidenhain's iron-haematoxylin and eosin. Magnification 425.

Fig. 3. An ovum showing basiphil granules. Fixed in Zenker's fluid; stained by Heidenhain's iron-haematoxylin and eosin. Magnification 550.

Fig. 4. Part of an ovum showing vacuoles left after removal of lipoid globules. Fixed in Zenker's fluid; stained by Heidenhain's iron-haematoxylin and eosin. Magnification 1200.

PLATE II

(The author is indebted to Professor Arthur Robinson for these two photographs.)

Fig. 5. Ovum showing numerous lipoid globules. Fixed in Flemming's fluid; tinted with eosin; magnification 500. It will be observed that the brittleness due to prolonged fixation in Flemming's fluid has led to rupture of the zona pellucida and part of the ovum.

Fig. 6. The same section; magnification 1000.

ABBREVIATIONS

b.g.	Basiphil granules.	*u.t.*	Uterine tube.
g.p.	Granular pole.	*v.*	Vacuole.
l.p.	Lipoidal pole.	*z.g.*	Zona granulosa.
p.b.	Polar body.	*z.p.*	Zona pellucida.
prn.	Pronucleus.		

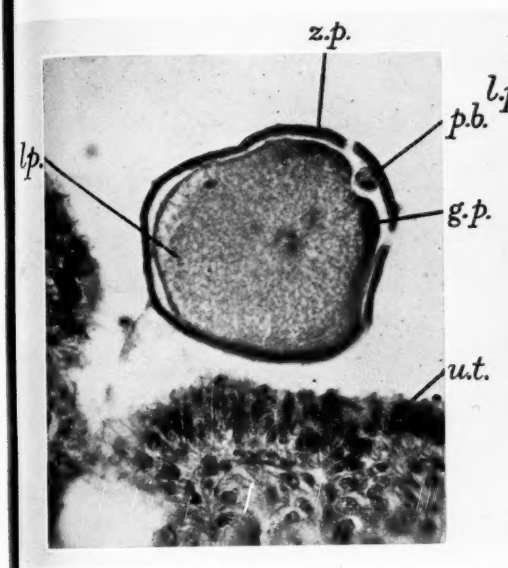


Fig. 1

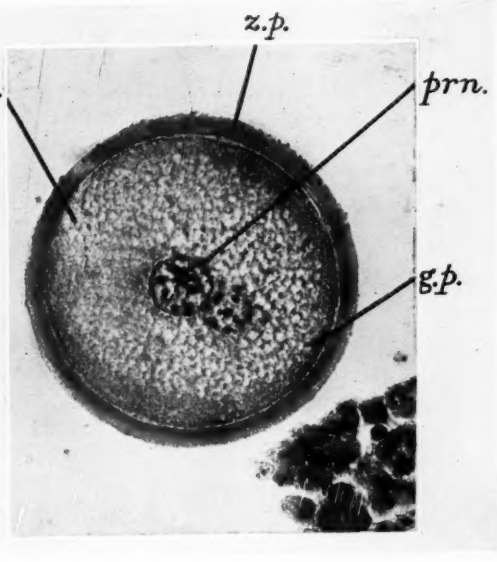


Fig. 2

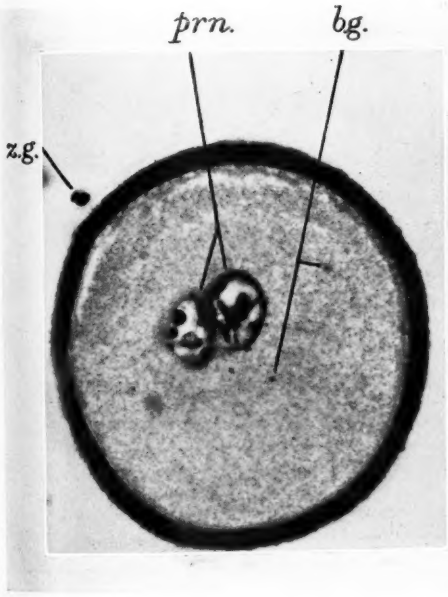


Fig. 3

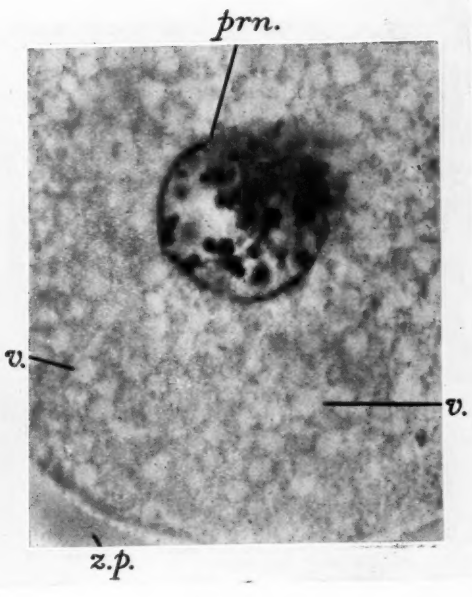


Fig. 4

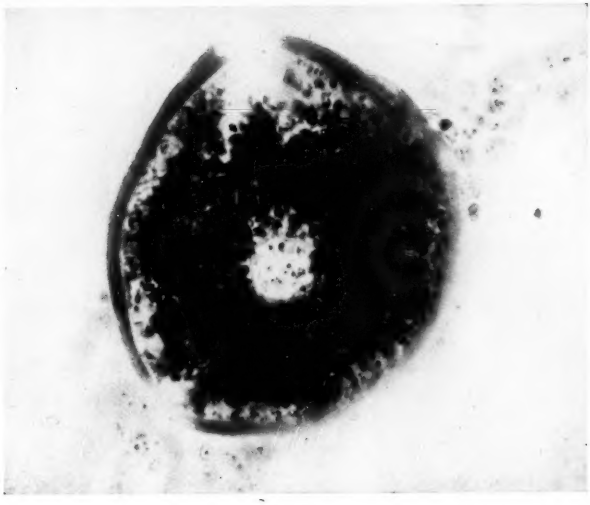


Fig. 5

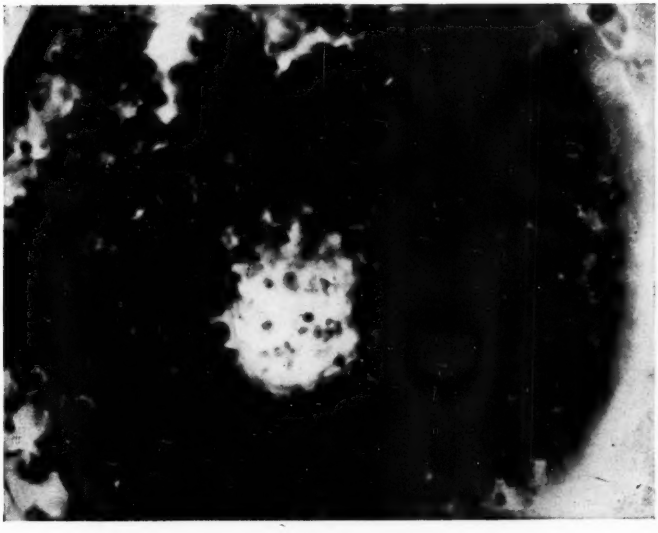


Fig. 6

AN ANATOMICAL ANALYSIS OF AN EXAMPLE OF POLYORCHIDISM

By E. S. J. KING, M.D., F.R.C.S.

Stewart Lecturer in Pathology, University of Melbourne, Australia

Although many examples of apparent polyorchidism have been described, but few will withstand critical examination. Clinical examination is obviously inadequate, since in many cases the second nodule present in or near the scrotum has been shown on investigation to be a cyst—(spermatocele, enlarged hydatid of Morgagni or hydrocele of the cord).

It is apparent that no case can be accepted in the absence of careful dissection and histological study. Review of the literature shows that so far but ten cases have been adequately reported.

In consideration of the rarity of the condition and because of certain special features the following case is considered worthy of record.

The patient, A.D., aged 21, complained of a "rupture" of the left side of several years duration.

On examination he was found to have a left inguinal hernia, not projecting beyond the external inguinal ring. The testis which was in the scrotum appeared to be normal (testicular sensation was present), but it was smaller than that on the right side. A small nodule in the region of the upper pole of the organ was freely mobile and was diagnosed as a floating epididymis. The testis on the right side seemed to be normal. The general development of the patient was that of a normal male adult.

At operation: a small peritoneal sac which extended almost to the external inguinal ring was found.

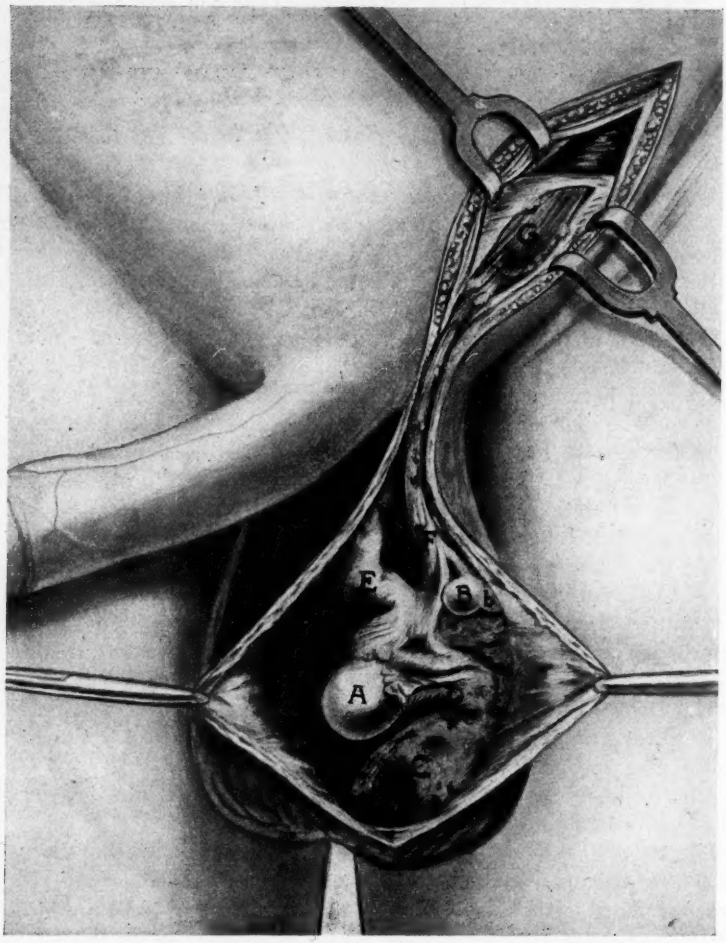
After dealing with this structure the testis was drawn into the wound in order to investigate it and the floating nodule.

Two testes were found in the scrotal sac, the smaller one being the nodule which was diagnosed as the "floating epididymis." A large hard mass of tissue was found in the base of the scrotum and the larger testis was attached to this by means of a portion of tissue which, on traction on the testis, became a firm band. Another similar band connected the testis with the pubic spine, and still another ran into the upper portion of the thigh, but this last was not fully investigated.

A firm band of tissue ran from the spermatic cord in the lower portion of the scrotum to both testes, and it was thought that the vas underwent division. Subsequent dissection, however, demonstrated that this did not occur.

The larger testis lay in the lower part of the scrotal sac, and the smaller

testis was in the upper part. They were about 2½ in. apart. They were attached to the posterior wall by a comparatively short border. The epididymis of the



Text-fig. 1. Diagram showing the relationships of structures as found at operation. *A*, larger testis. *B*, small testis. *b*, epididymis associated with smaller testis. *C*, mass of connective tissue and smooth muscle at the base of scrotum. *D*, gubernacular band connecting larger testis with the mass at the base of the scrotum. *E*, gubernacular band connecting the larger testis with the pubic tubercle. *F*, spermatic cord. *G*, hernial sac.

smaller testis was situated near the attachment of that organ, and together with the neighbouring portion of the "vas" it projected into the scrotal sac. The epididymis of the larger testis was not visible from the peritoneal aspect.

Since the testes were both small and probably imperfectly developed and because the mass of tissue at the base of the scrotum was thought to be pathological, they were removed together with the associated structures as far as the upper part of the inguinal canal.

MACROSCOPIC DESCRIPTION

The mass removed at operation presented a smooth (peritoneal) surface of the tunica vaginalis and a rough aspect (surface of separation from surrounding tissues).

It showed two ovoid bodies projecting from the peritoneal surface, the larger was situated in the lower portion of the scrotal sac and a smaller bilobed nodule in the upper part, consisting of testis and epididymis. There was thickening of the sub-peritoneal tissue in the portion corresponding to the attachment at the base of the scrotum.

The vas and accompanying structures were easily identified on the posterior aspect, and from the point at which the vas approached the bottom of the scrotal sac two raised folds (Plate I, fig. 1, A_L and A_S) were observed running to each organ. These were thought at first to be vasa deferentia, but dissection and microscopic examination showed that they were the vessels running to the organs.

Connecting the larger testis with the mass at the base of the scrotum (Plate I, fig. 1, *T*) was a thick band (Plate I, fig. 1, *G*) which was interpreted as being a remnant of the gubernaculum. Another band present (Plate I, fig. 1, portion of E_1) was that found at the operation to run to the pubic bone. These arose indefinitely from the posterior border of the larger testis.

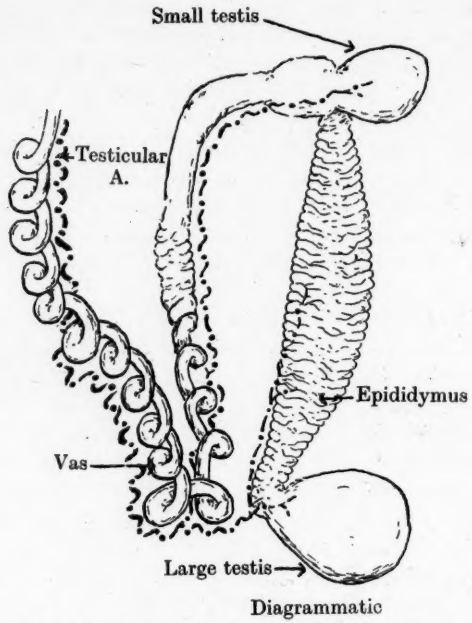
Dissection showed that the vas deferens descended in the usual position into the scrotal tissues to the region of the lower pole of the inferior testis and turned upwards abruptly (Plate I, fig. 2, *V*) until it reached the epididymis of the upper testis. From this organ the coiled tube then ran downwards to become the epididymis (Plate I, fig. 2, E_1) of the larger testis, thus reaching that organ (see Text-fig. 2). None of the tubule in this region resembled ductus deferens, but was entirely epididymal in nature.

The larger testis was an ovoid, slightly flattened body lying almost completely free in the cavity of the scrotal sac. It measured 2·6 cm. long × 1·8 cm. and was attached to the posterior wall for 1·8 cm. × 1·4 cm.

The epididymis corresponding to this organ was an elongate organ—on section—with the somewhat naked-eye appearance of a gland (e.g. pancreas or submaxillary gland), and possessing but a thin capsule. It extended from one testis to the other and measured 6 cm. in length. On cross-section at its middle it measured 1·1 cm. × 8 cm., at the distal end (near larger testis) it measured 5 mm. × 3 mm., and at the proximal end 5 mm. × 5 mm. It was embedded entirely in the tissue underlying the tunica and did not project into the scrotal sac.

The smaller testis was a smaller edition of the larger organ measuring 1·5 cm. × 1·2 cm. × 1 cm. The base of attachment measured 11 mm. × 6 mm.

The epididymis corresponding to this organ was a much more compact structure than the larger one, it projected into the scrotal sac and was covered by peritoneum. It measured 16 mm. × 9 mm. × 6 mm. This epididymis was measured as far as the constriction at its lower pole, which, macroscopically, separated it from the "vas." In structure, however, the vas and this epididymis merged gradually into each other, but the constriction is taken arbitrarily for the purpose of macroscopic description.



Text-fig. 2. Diagrammatic representation of the relationships of the various structures and the vessels shown in the photographs (Pl. I, figs. 1 and 2). Compare with fig. 2.

The structure connecting the "epididymis" with the vas measured 6 cm. in length, and having a serous covering, projected into the cavity of the scrotal sac.

It consisted of a highly coiled tube which microscopically resembled tissue of epididymis but merged into the structure of vas, since approaching the vas proper the coiled tubule became surrounded by a definite fibro-muscular coat (see subsequent descriptions).

From the point at which the vas deferens commenced to ascend towards the external inguinal ring the tubule became much thicker and less tortuous, so that this structure could be dissected out with ease. The length occupied

by the vas in the specimen was 8 cm., but the actual length of the tube was not determined. The diameter in its fully developed portion was 3 mm.

Vessels. Arteries and veins enmeshed the vas. At the lower part of the scrotum, these divided into two groups: (i) those accompanying the "vas" to the smaller testis (caused the fold in Plate I, fig. 1, A_S and Text-fig. 2), and (ii) those passing directly to the larger testis (Plate I, fig. 1, A_L; fig. 2, *A*).

Gubernacular remains. The strands of tissue passing from the testis to the base of the scrotum and to the pubic tubercle were thick and fibrous though not very sharply defined.

The mass of tissue at the base of the scrotum was a subperitoneal plaque, showing a number of small puckerings on the surface. It measured 3·6 cm. × 3·2 cm. in diameter and in thickness measured from 8 mm. to 2 mm. in different parts.

MICROSCOPIC DESCRIPTION

The *large testis* consisted of comparatively normal tubules which were lined by cells undergoing the usual metamorphosis from spermatogonia, through spermatocytes to spermatids (see Plate I, fig. 4). In the vast majority of the tubules there was no evidence of differentiation beyond this stage, but here and there a few apparently normal spermatozoa were observed. A layer of fibroblasts surrounded and defined each tubule in the normal manner and amongst the cells typical sustentacular cells of Sertoli were found (Plate I, fig. 5).

The intervening connective tissue was loose in texture, containing but few nuclei and fibrils. Groups of spheroidal cells with granular vacuolated protoplasm and central darkly staining nuclei—the interstitial cells of Hertwig—were present in this tissue (Plate I, figs. 3, 4, 5).

Blood and lymphatic vessels present manifested no abnormal features.

The *small testis* showed a much less advanced stage of development than the larger. It contained tubules which, on section, were somewhat smaller than those of the other testis and the cells of which were spermatogonia (Plate II, figs. 1, 2). There was no differentiation beyond this stage. The tubules were surrounded by a layer of fibroblasts, two to three cells thick. Between the tubules the tissue was loosely arranged, but was more cellular than that in the accompanying organ. Groups of interstitial cells—apparently normal—were present.

The *epididymis* (associated with the larger testis) consisted of tubules lined by an irregular double layer of cells (Plate I, fig. 6). The cells of the surface layer were not columnar but cuboidal. Their nuclei were centrally placed and cilia were present on the majority. The deeper layer of spheroidal cells was typical in character.

A layer of fibroblasts encircled the tubules and between these there was fibrous and smooth muscle tissue.

The tissue therefore closely resembled normal epididymis, except that the tubules were placed somewhat further apart and the inner cells were cuboidal rather than columnar.

The *smaller epididymis* consisted of tubules (see Plate II, fig. 3) lined by long columnar cells containing basally placed oval nuclei, and beneath them a layer of small spheroidal cells with round nuclei. Each tubule was surrounded by a layer of connective tissue and smooth muscle. Between the tubules was a loose connective tissue containing few fibroblasts and a few blood and lymphatic vessels.

The vas deferens in its distal portion consisted of the three layers of fibro-muscular tissue enclosing the mucous membrane (Plate II, fig. 4). This consisted in the part near to the epididymis of two layers, an outer layer of cuboidal cells and an inner layer of irregularly arranged columnar cells. In the former the nuclei were round and centrally placed, while in the columnar cells the nuclei were oval and situated in the basal part of the cell.

In the portion near the external inguinal ring the vas possessed only one layer of epithelium which was columnar in form and non-ciliated.

The gubernacular bands consisted of smooth muscle and connective tissue (Plate II, fig. 5).

The mass at the base of the scrotum consisted also of fibrous tissue with a considerable admixture of smooth muscle. The blood vessels were slightly thickened. Lymphatic vessels were numerous and normal in structure.

DISCUSSION

The literature of the subject of polyorchidism was considered in an article published in 1928 by Edington and Blacklock. They divided the reports into five groups: (i) General discussions, (ii) Pseudo-duplication, (iii) Clinical examination without operation, (iv) Operative demonstration without histological examination, (v) Operative demonstration with histological investigation.

Only those cases in which histological demonstration of the nature of the organs has been given can be regarded seriously, and of such cases only eight, prior to their own, were found by these writers.

An additional example is that reported by Ahlfeld, where the specimen was found at post-mortem.

Certain features of the specimen described here warrant special attention.

1. The two testes are attached to the Wolffian duct derivative "in series," i.e. not by bifurcation of the vas.

2. The terminal testis lay at the lower position in the scrotum. The gubernaculum was attached to it and was not attached to the upper testis.

3. The terminal testis was in close juxtaposition with the lowermost portion of the vas deferens.

4. The terminal testis (the organ furthest away from the inguinal ring) had nevertheless the shorter vascular pedicle.

1. As stated previously, it was thought at the operation that two vasa deferentia were present, arising by a bifurcation of the vas deferens where it lay in the upper portion of the scrotum. It was shown, however, that the structures responsible for this appearance were vessels. Dissection showed that the vas traversed the tissues to the region of the base of the scrotum, then turned abruptly upwards to the smaller testis with its epididymis, and from this the tube ran downwards again to the larger testis. The continuity

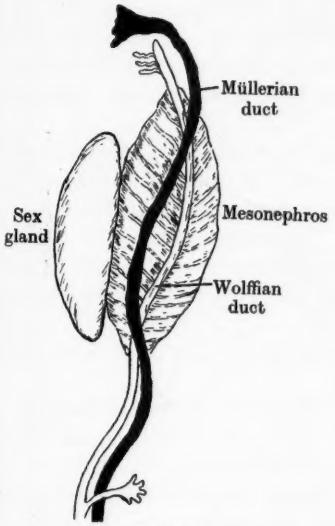


Fig. 3.

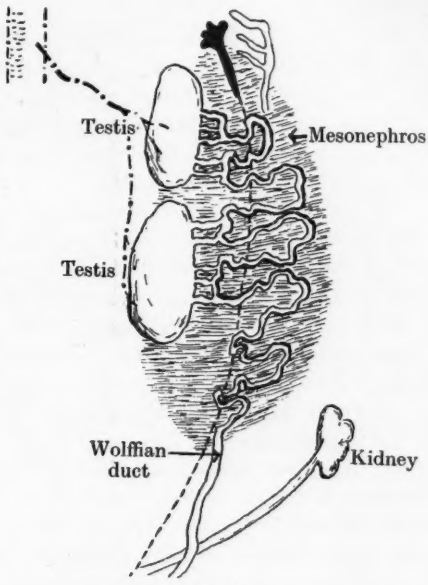


Fig. 4.

Text-fig. 3. Diagrams illustrating the embryological changes which are postulated as having occurred in this case. The sex gland in its original position in the medial aspect of the mesonephros.

Text-fig. 4. Subdivision of the gland, each portion having an artery derived from the spermatic vessel.

of the tube throughout its whole length was not determined with certainty, but the absence of any evidence of blockage—the healthy appearance of the cells, the evidence of normal cellular differentiation in the larger terminal testis (in which blockage of any portion of the duct would be expected to produce some effect), and the complete absence of any dilatation of ducts or any cystic changes—suggest that such continuity of the lumen was present.

The relative positions of the testes to the duct demonstrates that the duplication arose by a transverse fission of the genital ridge (see text-figs. 3, 4)

and that both became attached to and communicated with the Wolffian duct at different portions of its length and that these relative positions of attachment were retained.

2. The position of the terminal testis in the lower part of the scrotum raises the interesting problem concerning to which aspect of the genital gland the plica inguinale is attached.

Since the terminal testis is placed lowermost in the scrotum and it is this organ to which the gubernaculum is attached, it would appear that the plica inguinale is attached to the upper end of the genital ridge. The observation that the upper testis was more freely mobile than the lower lends support to this view.

The accepted view concerning the attachment of the plica inguinale is that this occurs at the lower pole. Certainly, in specimens examined, it is the lowermost pole to which the plica is attached. No direct evidence is available with regard to the earlier stages of development. It is possible, however, to draw certain deductions from the normal adult structure and from specimens such as this described.

The ductus deferens runs, normally, to the epididymis, overlying the "upper" pole of the testis, and from this the tubule is connected to the upper part of the posterior border. If the upper pole were the original lower pole, such a course would be readily explicable.

The specimen described suggests that the alternative explanation of the course and position of the duct after leaving the testis in the adult human being is possibly more correct.

However this may be, there can be little doubt as to the point of fixation of the plica inguinale in this case.

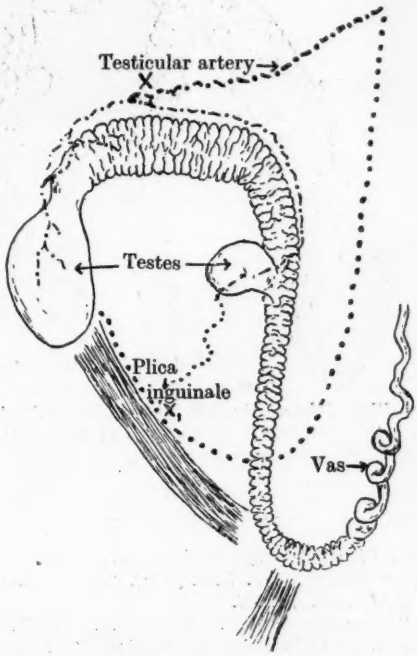
3. The close association of the terminal testis with the vas deferens is a corollary of the previous statement. The plica inguinale is attached inferiorly to the region of the internal inguinal ring and from here the plica gubernaculi runs to the bottom of the scrotum and elsewhere. Thus the testis normally becomes approximated to that portion of the vas which lies in the inguinal region and the vas together with the testis is drawn into the scrotum. In this specimen the association of the terminal testis with the lowermost portion of the vas, again suggests that it is the upper portion of the genital ridge to which the plica inguinale is attached.

4. The arrangement of the vessels is to be explained simply in a similar fashion. The testicular artery in the specimen accompanied the vas to the lower part of the scrotum and here divided into two branches. One passed immediately by a direct route to the terminal testis, while the other branch accompanied the tubule cranially to arrive at the other testis. The epididymis of the larger testis was supplied by the artery to the corresponding organ.

Since the spermatic vessels arise from the aorta, with the descent of the genital glands the vessel passing to the uppermost portion of the ridge should be the shorter.

When the upper testis becomes approximated to the vas lying in the inguinal canal, the vessel passing to this organ will again have a shorter course than the artery to the other organ, thus preserving the same relationships as are present in early development.

The degree of development of the gubernaculum was a marked feature of the specimen. They formed exceptionally strong bands as noted at operation, and histologically they consisted of a considerable quantity of smooth muscle and fibrous tissue (Plate II, fig. 5).

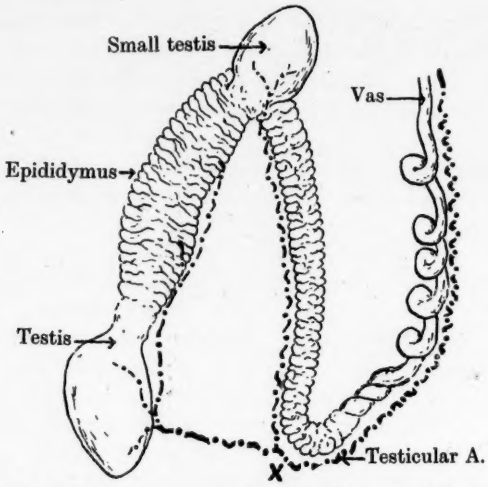


Text-fig. 5. Descent of the organs, the upper descending further than the lower owing to the attachment to it, of the gubernaculum. The point of bifurcation of the vessel *X* is regarded as being a fixed point in relationship with the terminal testis. The arrangement shown is purely diagrammatic. The dotted line indicates the position of the artery after further descent of the organs.

The mass of tissue at the base of the scrotum is probably due to hypertrophy of the tissue at the point of attachment of the scrotal gubernaculum. All the gubernacular tissues were tremendously in excess of what is usually observed.

The degree of differentiation of the cells in the two testes is interesting since in the terminal organ it has progressed to the formation of spermatids and a few spermatozoa, while in the other spermatogonia only are present. Both organs were in the scrotum, so that such factors as temperature (as

has been suggested) could not be the deciding factor. Differences in the site of origin from the genital ridge or differences in blood supply (the vessels to the smaller testis were smaller than those to the larger organ) have suggested themselves to account for the phenomenon, but no evidence in favour of such views is apparent.



Text-fig. 6. The final position of the structures in the scrotum. Owing to the descent from the abdomen (text-fig. 5) the vessel runs in juxtaposition to the vas deferens, and the point *X* remains in close relationship with the larger testis.

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Fig. 1. (*For* A_1 *read* A_8)

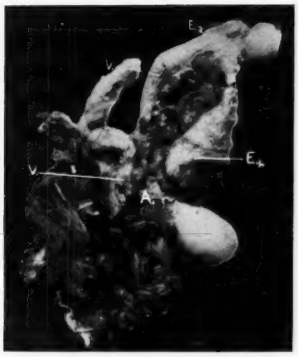

Fig. 2

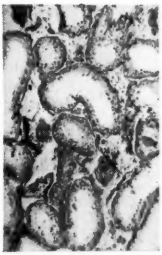

Fig. 3

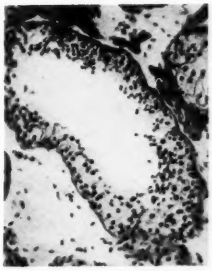

Fig. 4

Fig. 5

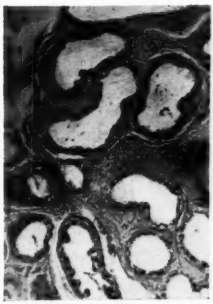

Fig. 6

UNIV. OF MICH.

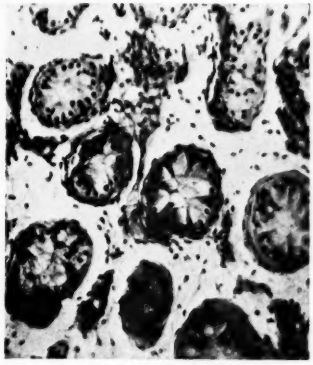

Fig. 1

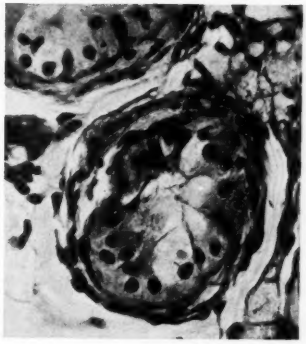

Fig. 2

Fig. 3

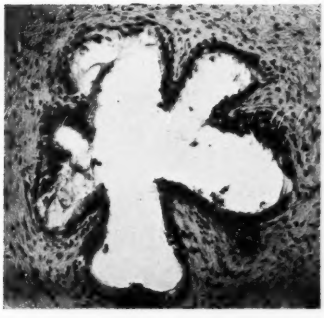

Fig. 4

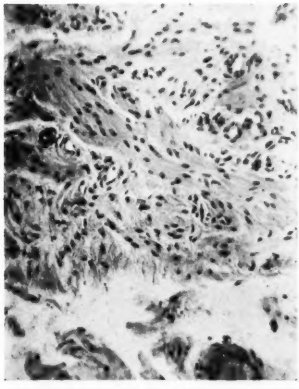

Fig. 5

EXPLANATION OF PLATES I AND II

PLATE I

Fig. 1. Photograph of the specimen after removal (viewed from the front). *L.T.* large testis. *S.T.* small testis. E_1, gubernacular tissue and lying behind this epididymis of larger testis. A_L, artery running to larger testis. A_S, artery running to smaller testis (cf. fig. 4). *T*, mass of tissue at the base of the scrotum. *G*, gubernaculum.

Fig. 2. Photograph of the specimen, viewed from behind. *V*, vas deferens. *A*, artery to larger testis. E_1, epididymis of larger testis extending from one organ to the other. E_2, epididymis corresponding to smaller testis.

Fig. 3. Photomicrograph of a section of the larger testis. ×54.

Fig. 4. Higher-power view of a tubule showing the differentiation of the cells. The intertubular tissue is loose in texture and contains but few cells. ×180.

Fig. 5. High-power view of tubules showing the differentiation of the spermatogonia, through spermatocytes to spermatids. Sustentacular cells of Sertoli are visible. Interstitial cells of Hertwig are also present. ×600.

Fig. 6. Photomicrograph of a section of the epididymis associated with the larger testis. ×60.

PLATE II

Fig. 1. Photomicrograph showing the structure of the smaller testis. Spermatogonia only are present in the tubules. Interstitial cells are present. ×180.

Fig. 2. High-power view showing the structure of the tubules. ×600.

Fig. 3. Photomicrograph of a section of the tissue extending between the "epididymis" of the smaller testis and vas deferens proper. ×60.

Fig. 4. Photomicrograph of a section of the vas deferens. ×110.

Fig. 5. Photomicrograph of a section of the gubernaculum showing the smooth muscle and connective tissue. The mass of tissue at the base of the scrotum had a similar structure. ×180.

THE NON-METRICAL MORPHOLOGICAL CHARACTERS OF THE SKULL AS CRITERIA FOR RACIAL DIAGNOSIS

PART III

THE NON-METRICAL MORPHOLOGICAL CHARACTERS OF THE SKULLS OF PREHISTORIC INHABITANTS OF GUAM

By FREDERIC WOOD-JONES
Honolulu

The skulls included in this series were excavated from burials in Guam by Dr T. C. Thompson and Mr H. G. Hornbostel, officers in the United States Navy. They were collected in January 1922, and the entire collection is in the possession of the Bernice P. Bishop Museum, to the authorities of which institution I am indebted for permission to examine them. The archaeological findings concerning these burials are as yet somewhat incomplete; but there can be no doubt that the burials are of the pre-Spanish period, and that they represent the indigenous race of Guam, uninfluenced by the influx and mixture of Spanish, Mexican, Philippino and Chinese that have produced the racial mixture of the present Chamorres. The outstanding feature of this series of skulls is its extraordinary homogeneity and the well-differentiated cranial and facial type that prevails in all individuals. In non-metrical morphological features, as in gross characters, these skulls differ widely from the Polynesian type, and in their general form they may, for the present, be assumed to represent an insular race, the place of origin and affinities of which are so far undetermined[1].

In the series available to me at the time I made my examination there were the remains of ninety-two persons. Of these, only six were sufficiently complete for entire skulls to be associated with more or less intact pelves. In these examples cranial sexual characters were so well differentiated that the sexing of the remainder of the series by cranial characters alone has a comparatively high guarantee of accuracy. Thirty-three skulls could confidently be regarded as being female and thirty-three as male: the remaining twenty-six were too fragmentary or too indeterminate in type to justify any precise diagnosis of sexual or morphological characters. The number of skulls from which deductions may be drawn is therefore small, but perhaps this defect is in part compensated for by the remarkable homogeneity of the series.

(1) *Cranial Form.* The typical skull may be described as a massive and symmetrical cranium with a contour in the norma verticalis most nearly represented by Sergi's sphenoid and with a somewhat angular outline. The typical female skull is distinguished by its more regular oval form. The occiput is rather steep, the forehead square and the temporal fossae moderately well filled.

[1] The examination of a series of crania in the Museum of the University of Sydney leaves no doubt that these skulls from Guam are of the same racial type as those from New Caledonia and the Loyalty Islands. F. W.-J.

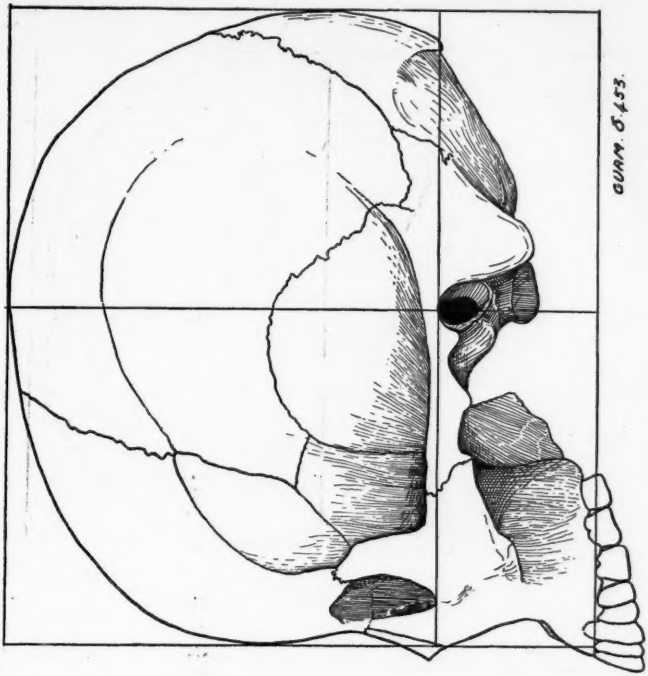

Fig. 2. Norma lateralis.

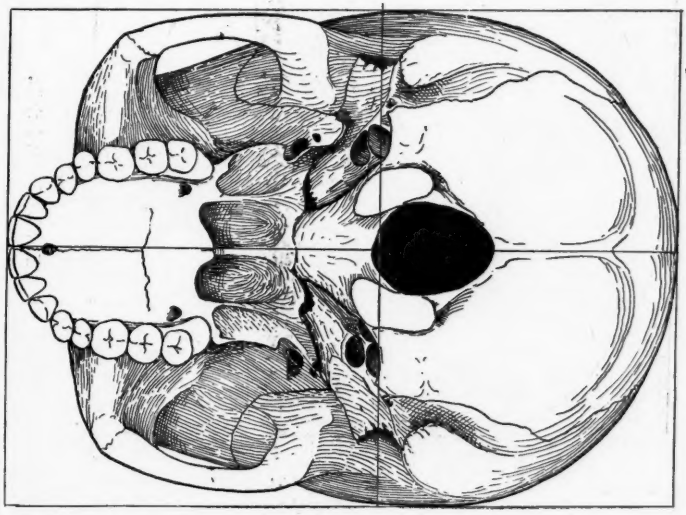

Fig. 1. Norma basalis. Typical Guam male. Sexed from the pelvis. All figures reduced to half natural size.

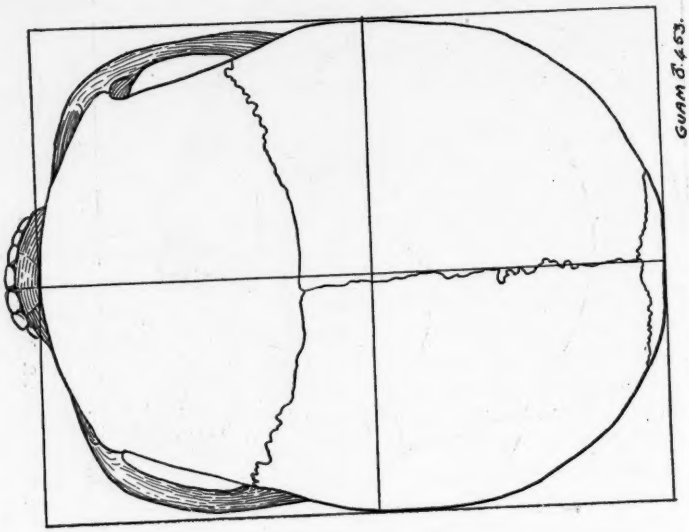

Fig. 4. Norma verticalis.

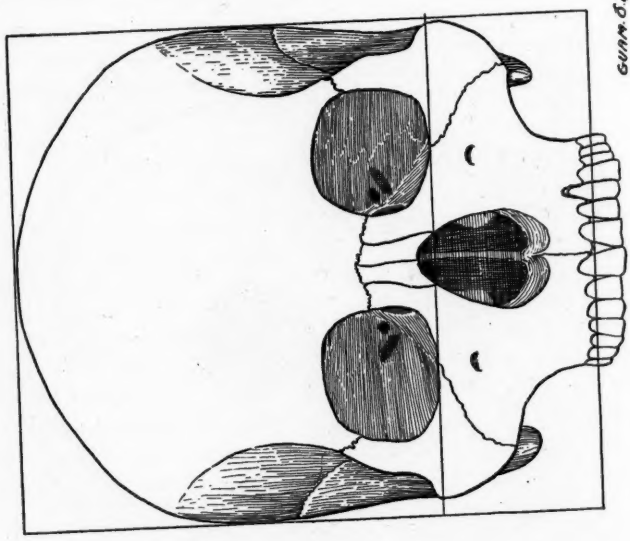

Fig. 3. Norma facialis.

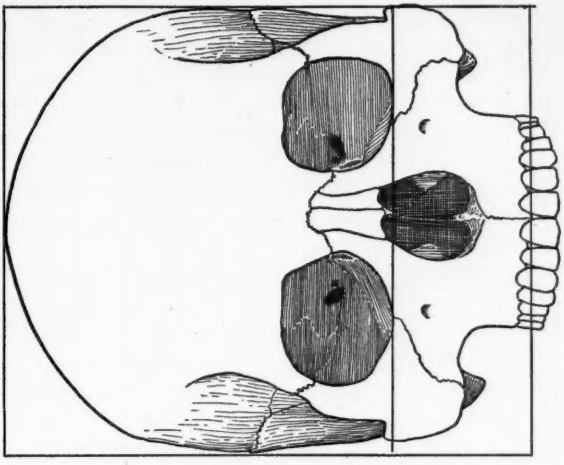

Fig. 6. Norma facialis.

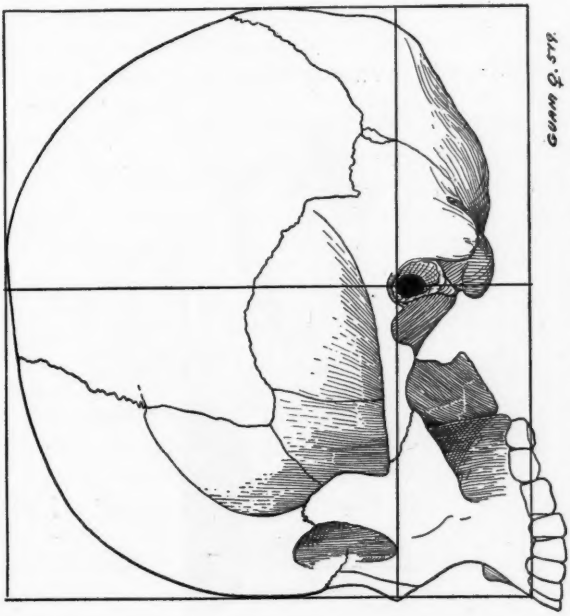

Fig. 5. Norma lateralis. Typical Guam female sexed from the pelvis.

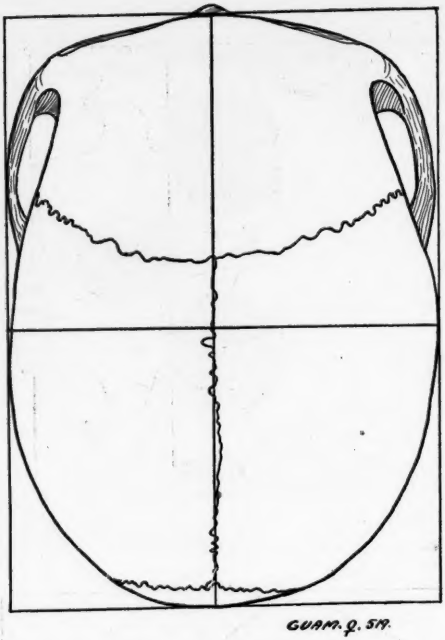

Fig. 7. Norma verticalis.

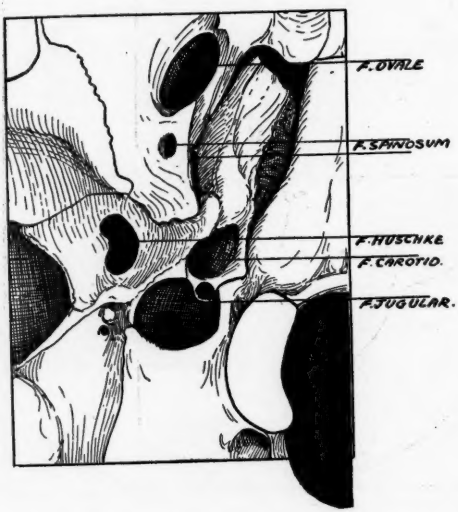

Fig. 8. The region of the foramen lacerum medium to show the type common in skulls from Guam.

(2) *Cranial Asymmetry.* Of the whole series of skulls as many as 42 per cent. showed no obvious degree of asymmetry as judged by inspection in the norma verticalis. Symmetry, so estimated, was present in 36 per cent. of the males and 48 per cent. of the females. Normal asymmetry occurred in 44 per cent. of the total series (50 per cent. of the males and 38 per cent. of the females). Reversed asymmetry was present in 14 per cent., and in this feature the sexes showed equality.

(3) *The Sutures* in all cases were of a very simple pattern. In 30 per cent. of cases the sutural pattern was noted as being conspicuously free from complications. No case of metopic suture was present in this series.

(4) *Ossa Suturarum.* Womian bones are infrequent and no large or striking inclusions were present.

Lambdoid ossicles were present in 23 per cent. of the whole series (10 per cent. in the males and 36 per cent. in the females). No case of a true interparietal bone was met with. The ossicles were multiple in 10 per cent. of the total series.

Ossicles occurred in the occipito-mastoid suture in only 3 per cent. of the total series. Coronary ossicles were entirely absent.

(5) *The Pterion* was of the normal type in every example, and in 50 per cent. of the cases it was noted that there was an unusually elongated alisphenoid-parietal contact.

(6) *Epipteric Bones* were present in only 6 per cent. of the total series, there being three times as many cases in females as in males. In only one instance—that of a female—was the bone confined to one (left) side.

(7) *Supra-orbital Foramina, Notches and Grooves.* Bilateral supra-orbital notches, for the most part extremely shallow, were present in 86 per cent. and bilateral foramina in only 5 per cent. The condition differed upon the two sides in 9 per cent. and in these asymmetrical examples a notch was present on the right and a foramen on the left in 6 per cent., the reversed condition being present in 3 per cent. Accessory notches or foramina were present in 32 per cent. of the total series: they occurred bilaterally in 7 per cent., on the right side only in 18 per cent., and on the left side only in 7 per cent.

(8) *Anterior Ethmoidal Foramen.* In only thirty skulls could the site of the foramen be determined beyond all possibility of doubt. Of these examples the foramen perforated the fronto-ethmoid suture in sixteen (53·3 per cent.), and the frontal above the suture line in fourteen (46·6 per cent.). No sexual difference in the site of exit was evidenced in this small series.

(9) *Sutures of the Inner Wall of the Orbit.* In no case was any anomaly recorded.

(10) *Spheno-maxillary Fissure.* The fissure was narrower than the European normal in 59 per cent. It was of normal width in 32 per cent., wider than the average in only 2 per cent. and of the narrow type but with expanded extremity in 7 per cent.

(11) *The Orbits* are most commonly only very slightly oblique. Such a con-

dition was present in 66 per cent., and in 9 per cent. of the cases in which there was obliquity this condition was more apparent on the right side than on the left. In 34 per cent. the axis of the orbits were adjudged to be level. The shape of the orbits is conspicuously square, and "square and nearly level" is the description that applies to the orbit typical of the series.

(12) *The Infra-orbital Canal.* A single discrete foramen gave exit to the nerve in 55 per cent.; a minute accessory foramen was present in 45 per cent. In 31 per cent. this minute accessory was present on both sides and in 14 per cent. it was unilateral—the right and left sides being equally represented. In only one case could the canal be described as double and here the duplication was confined to the right side.

(13) *The Form of the Jugal.* One of the most striking features of this series of skulls is the massiveness of the malars and the eversion of their lower margins. Combined with this is great thickness of the lower margin of the zygomata and a sharply angled (instead of curved) junction of the zygomata with the facial portion of the skull. Subdivision of the malars was not met with.

(14) *Nasal Bones.* The nasal bones were noted to be narrow at their upper extremities in 50 per cent. Inequality of the upper extremities occurred in 40 per cent., and the right bone was broader than the left four times as often as the reverse condition. In 14 per cent. of cases the upper extremities were synostosed in some degree: the condition was present in both sexes but never in young skulls.

(15) *The Narial Aperture* is typically a low ovoid. The narial margins are practically always double, the ridges being low and their separation considerable in 70 per cent. In 23 per cent. the divergence of the margins and the continuity between the superior alveolar surface and the floor of the nasal chamber reached the condition that is best described as guttered. In only 7 per cent. were the margins approaching the condition that can be termed sharp and these more sharply marked margins were all present in the skulls of women. There is a conspicuous degree of apparent subnasal prognathism in the typical skull.

(16) *The Nasal Septum.* The condition of the septum could be recorded in so few cases that the figures probably lack any significance.

(17) *The Foramen Ovale.* The posterior wall of the foramen ovale was abnormally thin or reduced to a mere spicule of bone in 9 per cent. of all cases and in this feature the sexes were equal. No case was met with in which the posterior wall was altogether lacking; but confluence of the foramen spinosum and foramen ovale was present in as many as 11 per cent., no sexual distinction being shown. The foramen, when otherwise normal, was recorded as unusually small in 33 per cent. and as unduly large in 20 per cent.; these anomalies in size were apparently not correlated with any corresponding variations in the foramen of Vesalius.

(18) *The Foramen of Vesalius.* The foramen of Vesalius was present in only 9 per cent. of the total series, and in only one case was its occurrence unilateral.

(19) *The Foramen Spinosum* was present as a completed bony canal in 42 per cent. of all the cases in which its condition could be diagnosed with certainty. It was incomplete on both sides in 18 per cent. and incomplete on one side or the other in 29 per cent. In 18 per cent. it was complete on the right and incomplete on the left and in 11 per cent. it was complete on the left side only. In 11 per cent. it was confluent with the foramen ovale.

(20) *The Spina Angularis Sphenoidei.* The spine is typically a large but clumsy prolongation of the angle, lacking definition as a sharp discrete prominence or even as a defined ridge. In the great majority of skulls its most noteworthy feature is its overflow over the petrous posteriorly. This condition may occur upon one side or both. In the example figured (see fig. 8) the features depicted are bilateral.

(21) *The Laminae Pterygoidei.* The lamina lateralis is typically wide-splayed, but not greatly enlarged laterally. Both laminae are distinguished by their thickened lower margins, their stoutness, and the marked muscular impressions. The tendency to the formation of a pterygo-spinous bar is displayed only in a manifestation to develop a ridge to the medial side of the foramen ovale.

(22) *The Jugular Foramen* was recorded as approximately equal upon the two sides in 20 per cent. of cases. The right canal was considerably larger than the left in 64 per cent. and the left larger than the right in 16 per cent. No sexual differences were detected.

(23) *The Tympanic* as it forms the floor and the orifice of the external auditory meatus is notably under-developed in this series. This under-development finds partial expression in the high frequency of the foramen of Huschke (32 per cent.) and the number of cases (20 per cent.) in which the styloid processes fail to be present. The external auditory meatus is typically large and ringed round by a thin plate of bone which fails markedly in its lateral development. The tympanic was noted as being of normal or somewhat subnormal massiveness in 44 per cent. and of striking under-development in 56 per cent.

(24) *The Foramen of Huschke.* This was present as a large gap in the floor of the external auditory meatus in no less than 32 per cent. of the entire series. In 27 per cent. the foramen was bilateral and in 5 per cent. it was confined to one side, there being an equal number of unilateral occurrences on either side.

(25) *The Styloid Processes* were present in 80 per cent. of the total series. They were of normal or more than normal development in 36 per cent., small in 36 per cent. and rudimentary in 8 per cent. In 20 per cent. they were entirely absent and this condition was confined to the female.

(26) *The Posterior Condyloid Foramina,* when present, are usually small in size. Small bilateral foramina were present in 65 per cent. of all the cases in which the condition could be determined with certainty. They were completely lacking in 9 per cent. A single foramen was present on the right side only in 17 per cent. and on the left side only in 9 per cent.

ON A POST-FRONTAL AND ORBITAL ELEMENTS IN A YOUNG GORILLA SKULL[1]

By M. F. ASHLEY-MONTAGU

The development and the conformation of the bones in the pteric region of the Primate skull is of great morphological and phylogenetic interest. As is well known to anatomists, in the Primates four bones normally take part in producing the pterion, namely, the posterior inferior angle of the frontal, the anterior inferior angle of the parietal, the posterior superior angle of the alisphenoid, and the anterior superior margin of the squamous bones, whilst in some South American monkeys a fifth bone, the malar, is added. The types of articulation and the form of these bones is subject to a considerable amount of variation in most Primate genera, the Lemuroidea, the Cebidae, and the Gorillidae alone exhibiting a generally constant type of pteric form. Among the various races of Man there is a good deal of variation in the form of the pterion, but among whites generally the moderately broad spheno-parietal articulation is a pretty constant feature of the skull. In the Mallicolese, however, the fronto-temporal articulation occurs in about 48 per cent. of crania. In Man, but only exceptionally in the rest of the Primates, accessory bones not infrequently occur upon the site of the antero-lateral fontanelle. These bones may border upon the frontal, parietal, alisphenoid, and squamous, or upon any two or three of these bones. Such accessory bones, of which there may be one or several, are known as *epipteric bones*. It has been suggested by the majority of writers on this subject that the fronto-temporal articulation in Man is due to the annexation by the temporal, or more rarely by the frontal, of an epipteric bone, thus preventing the contact between the alisphenoid and the parietal bones (1), (2), (3), (4), (5), (6). That this may provide a satisfactory explanation of the fronto-temporal articulation may be allowed for some cases, but that such an explanation cannot hold good for the majority of cases is certain (7), (8), (9), (10). It can, for example, be demonstrated that the fronto-temporal contact in the Mallicolese is not brought about by the annexation of an epipteric bone, but by perfectly normal agents which are peculiar to this people.

Some authors have seen in the pteric bones the reappearance of the *post-frontal* bone of the pre-mammalian skull (11), (12), (13), *et vide* (15). But an examination of the embryological development of the bones constituting the pteric region, and the situation and history of epipteric bones renders it quite certain that epipteric bones have no connection whatsoever with the primitive post-frontal bone and are therefore inaccurately described as such. This is a matter to which we will return.

[1] I have to thank Prof. J. H. McGregor, of Columbia University, New York, for his kindness in allowing me to examine the skulls here described.

It is not widely known among anatomists that the post-frontal bone is a constant element of the developing human skull. For some extraordinary reason most modern text-books of anatomy and embryology make no mention of the post-frontal element of the human foetal skull in spite of the fact that a constant and independent centre of ossification of this bone is present in every case, and the bone itself may generally be observed up to the end of the third foetal month, and not rarely in the skulls of newborn children. This is the more surprising since the bone was accurately described by Fallopia as far back as the year 1600 (14), since when it has been discussed by not a few investigators (15).

The centre of ossification for the post-frontal bone arises very early in the development of the membranous bones at a point which may be identified in the adult skull as the posterior inferior angle of the frontal (15), (16). The

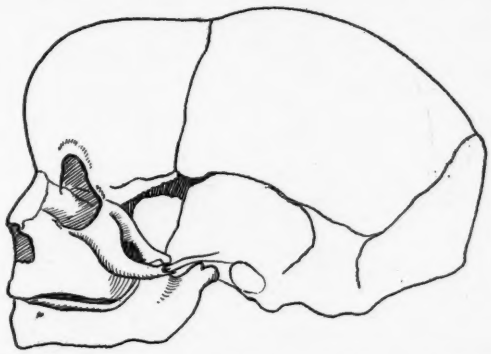

Fig. 1. Skull of a newborn child exhibiting the post-frontal element in its external relations and showing the possibilities of growth in the parietal vicinity. (After Jhering.)

bone generated from this centre lies close to and in front of the antero-lateral fontanelle and superior to the jugal process (16), (fig. 1). The union of the post-frontal with the frontal is normally complete by the end of the third month of development. Occasionally, however, a failure of union takes place, and in newborn skulls the bone has not infrequently been observed as an isolated element extending backwards above the jugal process from the point which later becomes the anterior margin of the orbito-frontal process to the coronal suture at the inferior lateral angle of the parietal bone (fig. 2). No case has, however, been described in which the post-frontal element was found independent later than the stage of birth, either in Man or in any of the other Primates, nor has any previous investigator been able to show exactly what part this element plays in the formation of the inner lateral wall of the orbit. In this communication a unique case of the fully developed post-frontal element will be described in a young gorilla skull, and some light will be thrown upon the contribution of this bone to the formation of the orbit.

The skull described is that of a young *Gorilla gorilla* from the Cameroons of West Africa, in which the deciduous dentition is in process of giving way to the permanent teeth. All the sutures are open, with the exception of the internasal suture which is just closing.

Maximum length of the skull ...	138 mm.
Maximum breadth of the skull...	102 mm.
Orbital height	40 mm.
Orbital breadth	36 mm.
Auricular-vertex height... ...	61 mm.
Bi-pteric width	70 mm.

The post-frontal element is a bone some 32 mm. high by 28 mm. broad, situated in the left fronto-temporal region and occupying an area extending from about 10 mm. above the level of the fronto-jugal suture to the superior

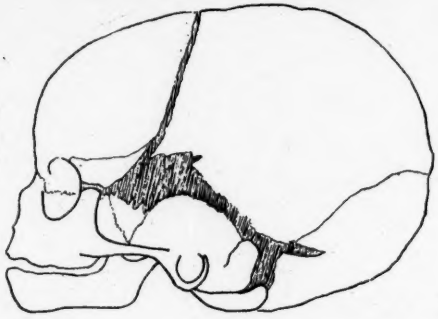

Fig. 2. Skull of a newborn child exhibiting the post-frontal element in its external relations. (After Ranke.)

margin of the alisphenoid bone (fig. 3), and upon the inner lateral wall of the orbit occupying an oblong area some 22·5 mm. high and 13·5 mm. broad (fig. 5).

The structure of the malar, alisphenoid, and squamous bones on both sides of the skull are as alike as they could possibly be. A posterior superiorly situated spicule of the alisphenoid bone on the right side alone rises slightly higher than the similar spicule on the left side, and causes the anterior superior angular suture of the squamous to be slightly shorter on that side than it is on the left. On the right side too the squamous at its contact with the frontal is spiculated whereas on the left it is not, but runs comparatively even.

The height of the wing of the sphenoid from the inferior acute alisphenoid point to the anterior spheno-malar point is identical on both sides of the skull, 26·5 mm.

The height of the wing of the sphenoid from the same point to the posterior superior spheno-squamous point is 30 mm. on the left, and 33·5 mm. on the right side.

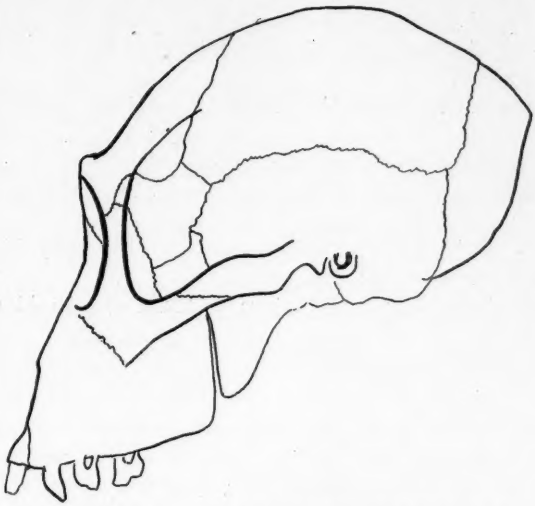

Fig. 3. Dioptographic projection of the left side of the skull made in the nasion-porion plane showing the situation and relations of the post-frontal element.

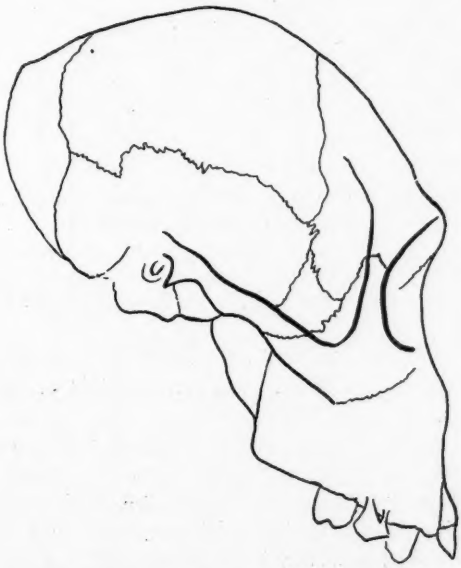

Fig. 4. Dioptographic projection made in the nasion-porion plane of the right side of the skull showing the normal configuration of the bones.

The height of the wing of the sphenoid from the same point to the mid-point of the superior alisphenoid suture is the same on both sides, 23 mm.

The breadth of the alisphenoid at the middle of its body is the same on both sides, 15·5 mm.

The distance of the alisphenoid from the fronto-jugal level is 23·5 mm. on both sides.

The spheno-malar suture is 14 mm. long on both sides.

The length of the alisphenoid suture from point to point is 20 mm. on both sides.

The length of the spheno-squamous suture on the right side is 20 mm., and on the left side 23·5 mm.

The length of the malar-frontal suture is 22 mm. on both sides.

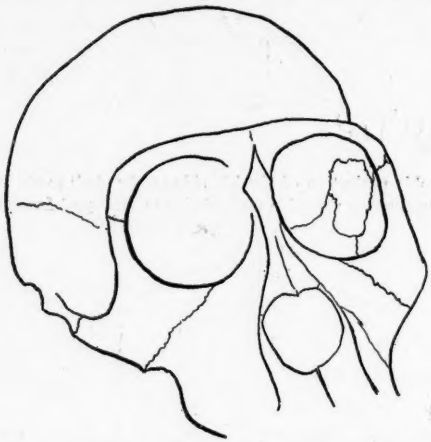

Fig. 5. Dioptographic projection in a free plane showing the internal situation and relations of the post-frontal element.

The fronto-temporal suture and its counterpart on the left side is 11 mm. long.

From these figures it is to be observed that the form and size of the bones and sutures on both sides of the skull are almost in every case identical in their proportions.

A difference in the form of the antero-lateral angle of the parietal bone, however, is at once perceptible. On the right side of the skull the coronal suture meets the squamous some 6 mm. below the fronto-jugal level to form with the approximately horizontal parieto-squamous suture an angle of about 90°. On the left side, however, the coronal suture, which inclines slightly more forward inferiorly, is cut short some 10 mm. above the fronto-jugal level to meet the posterior superior point of the new bone, which latter, from

this point, runs obliquely backwards to meet the anterior superior angular point of the squamous at an angle of some 60°, thus trisecting the antero-lateral angle of the parietal. The parietal suture here is 11 mm. long. It seems then that the posterior superior section of this new element has made a slight but appreciable inroad into the territory normally occupied by the antero-lateral angle of the parietal bone.

From the posterior superior point the infra-frontal suture, as the suture which separates the post-frontal and frontal bones from one another may be called, runs superiorly concavely forwards to the orbito-temporal point for some 15 mm., to continue obliquely forwards and downwards some two-thirds of the way into the orbito-frontal process for some 13 mm. Thereafter the sutural relations of this element are as in the normal frontal bone.

In the lateral wall of the orbit the new element is represented by an oblong bone 22·5 mm. in height and 13·5 mm. in breadth, perfectly accommodated to the rounded orbit (fig. 5). Superiorly it articulates with the frontal like the three sides of a square over an area some 9 mm. × 13·5 mm., and inferiorly for some 13·5 mm. with the antero-posterior oblique malar, 14 mm., and the sphenoid inferiorly, 10·5 mm., and posteriorly, 6·5 mm., for posteriorly there is a spicule of the sphenoid which corresponds to the spicule of the alisphenoid on the outer wall of the skull. The medial wall and the floor of the orbits are broken away, but as far as can be observed there is no other abnormality present in either of the orbits.

From the above description, and in view of the known structure and relations of the normal foetal post-frontal element, it would appear that we have here a rare case of failure of union between the post-frontal element with the frontal and its persistent development as an independent bone. When, as in the present case, such a condition occurs it is discovered that the post-frontal element occupies an area which is normally assumed by the complete inferior lateral part of the frontal bone, and that this element plays a very definite rôle in forming the inner lateral wall of the orbit, as well as the posterior inferior lateral division of the orbito-frontal process.

That the orbital element arises from the same source as the external element is shown by the fact that at the malar and alisphenoid borders they are perfectly evenly united with one another, whilst the passage of concentrated light through both divisions reveals the diploic structure common to lamellar bones arising from the same centre.

At this stage it might be well to posit the question whether the interpretation of this element as a post-frontal bone fulfils the demands of valid inference from the known facts of our subject, and whether there are any relevant facts in this instance, or in any other, which would suggest an alternative interpretation? In order to answer this question the only other characters of interest presented by this skull will now be considered, together with a brief review of the evidence for an alternative interpretation.

At the bregma there is a small maple leaf-shaped Wormian bone 9·5 mm.

in length and 13 mm. in breadth, and there is evidence that another bone triangular in shape some 20 mm. in breadth and 10 mm. in length has independently occupied the area immediately anterior to the first bone. From its appearance, however, it may well be regarded as part of the normal osseous bregmatic membrane undergoing its final ossification with the frontal (fig. 6).

In the left coronal suture some 12 mm. from the extremity of the maple-leaf Wormian bone there occurs another small Wormian bone about 3 mm. broad and 1 mm. long. For some 26 mm. posterior to the bregmatic Wormian

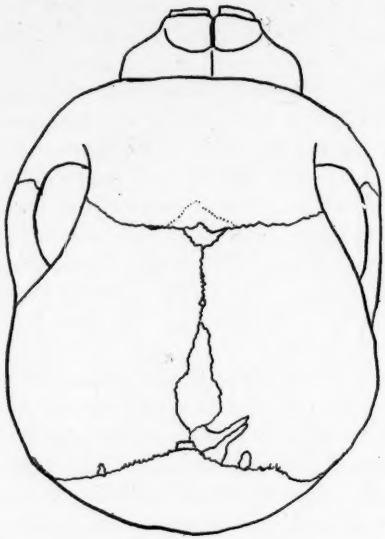

Fig. 6. Dioptographic projection made in the nasion-porion plane of the vault of the skull showing the fontanelle and other Wormian bones.

bone the sagittal suture, quite normally denticulated, extends, with a single Wormian bone some 2 mm. square in the posterior two-thirds of its length, until a large Wormian bone roughly flask-shaped in appearance is encountered upon the site of the parietal fontanelle. This bone is 30 mm. in length, and 6 mm. broad at the neck which is 12 mm. long, and 15 mm. broad at the body which is 18 mm. long, and curves outwards and downwards on either side to terminate at a point which just fails to articulate with the lambdoid suture by some 6 mm., the parietal and a small Wormian bone, some 3 mm. long and 6 mm. broad intervening inferiorly and to the left. On the right side between the terminus of the sagittal suture and immediately inferior to the flask-shaped Wormian bone, two additional large spiculated Wormian bones occur, extending laterally and upwards into the posterior superior angle of the parietal. The superior measures 18 mm. in length, and in its inferior broadest

part is some 7 mm., the inferior measures 16 mm. in length, and in its broadest part is 7 mm.

The lambdoid suture is normally denticulated, one small Wormian bone occurring in its left lateral division, and another some 6 mm. long and 3 mm. broad occurring in its right medial middle half.

Wormian bones or any other unusual characters occur neither at the asterion nor elsewhere in the skull.

The occurrence of Wormian bone, particularly at the bregmatic, parietal and occipital fontanelle regions, together with the unique form of the post-frontal element, would suggest a possible general cause of a pathological or otherwise abnormal nature for the appearance of this latter bone, and that it is perhaps properly to be regarded as a Wormian bone. On the other hand, the relation between the post-frontal element and the other Wormian bones may be quite fortuitous, so that it would be necessary to resort to a separate explanation in order to account for them in each case. But that some abnormal cause is responsible for the development of this element goes without saying, and that there is a possible relationship of associated cause with the fontanelle bones is probable though indeterminable. But whether or not such a relationship can be shown to obtain, the post-frontal element can, in any case, still be interpreted as functionally or in origin equivalent to a Wormian bone. Thus, for example, it is conceivable that the post-frontal ossificatory centre was early destroyed, or for some reason failed to develop, and that a new and independent centre then appeared which successfully opposed its stress to the terminal ends of the surrrounding bones, performing in every way the functions of the post-frontal element. Even so we are still forced to regard this element as a post-frontal bone, for if it has arisen as the result of the failure of development of the true post-frontal, then clearly it occupies the place that such a *persistent* element would have occupied, with the possible exception of the orbital division, which, regarded as the cover-plate of a gap caused pathologically or accidentally and independently of the external division, has therefore no connection with the post-frontal element at all. In the latter event the external element alone could be regarded as a simulated (Wormian bone) or persistent post-frontal bone. But an examination of the normal relations of the outer and inner orbital walls in the post-frontal area renders such an assumption quite unnecessary and the fact quite certain that in the skull under consideration the post-frontal element as an independent bone contributes to the formation of the inner lateral wall of the orbit an area of bone delimited above by the roof of the frontal, and antero-superiorly by the internal curving orbito-frontal process, antero-inferiorly by the malar, postero-inferiorly by the sphenoid, and posteriorly by the declining roof of the frontal.

There is every reason in this case to regard the outer and inner elements as intimately connected and as derived from identical sources, and not as arising dissociatedly.

A possible point in favour of the Wormian bone theory of the origin of

this element may be derived from the fact of the trisection of the antero-lateral angle of the parietal by a covering ingrowth of the new element, which does not correspond to the normal distribution of the frontal bone at this place. Actually, however, there is no reason why the post-frontal element should not of itself make good or assume part of the territory upon which it debouches, particularly when that element remains free and ununited. The probability of this may better be realised by a glance at the position occupied by the post-frontal element in the parietal area as shown in fig. 1.

The objections to the Wormian bone theory are (1) that Wormian bones never occur within the orbit, (2) that Wormian bones are never found as doubled bones, and (3), when large gaps are to be covered, a number of Wormian bones usually perform that function (17), and in this case it is almost certain that the orbital and external elements would have arisen as distinct and separate bones. There are, of course, a number of objections to these objections, but when these have been carefully weighed the balance of probability is in favour of this bone being a true post-frontal element as against a single gigantic Wormian bone.

We may now consider the suggestion that this element may possibly be an epipteric bone.

An epipteric bone is essentially a fontanelle bone specific to the antero-lateral region of the skull. It may border, as has already been pointed out, upon any of the four bones of the pteric region (18), and, according to various authors, epipteric bones may arise from an osseous granulation of the chondral tissue in the immediate vicinity of the ala temporalis (12), or after birth from an independent centre of ossification (9), (15), (17); or they may arise by becoming detached from the primitive cartilaginous blade which, extending from the clinoid process, reaches the pteric region in the foetus and, after the latter's resorption, continues an independent secondary development in the associated membranous tissue (19); or in the post-natal skull as osseous plates from independent centres of ossification in order to supplant the membranous fontanelle gaps which for some reason have not been covered by the surrounding bones (9), (15), (17); or they may be regarded as the detached angles of the adjoining bones possessing no morphological significance whatever (6); and, finally, they may be regarded as atavistic post-frontal bones (11), (12), (13), *et vide* (15).

Whichever of these views as to the origin of the epipteric bones we adopt it is clear that the bones themselves are characterised by the fact that they occur upon the site of the antero-lateral fontanelle, never once bordering upon the malar or orbito-frontal processes. This fact alone is sufficient to exclude the possibility of the present post-frontal element from being considered as an epipteric bone.

As for the view which sees in the epipteric bones the reappearance of the pre-mammalian post-frontal bone, it is a fact worthy of note that all those authors who have made such a claim were completely unaware of the fact

that, as far as we know, the post-frontal bone is present in the developing skull of probably all Primates, and certainly of all Men. Accordingly they were likewise unaware of the fact that were this bone to persist in Man it would occupy a place, not between the pteric bones, but a position somewhat below the inferior temporal crest extending from the coronal suture at the parietal and above the alisphenoid to a point superior to the jugal at the posterior margin of the orbital process, a position which may be easily educed by an examination of fig. 1, together with the same area in an adult human skull. That an epipteric bone may arise as a detached part of the post-frontal element is quite possible, but it is not thereby converted to the rank of a post-frontal bone. Clearly, an epipteric bone cannot possibly be identified as a post-frontal bone or *vice versa*.

Thus upon the basis of the foregoing considerations we must conclude that the young gorilla skull here described exhibits an anomalous bone which is to be distinguished from a Wormian or epipteric bone, and which, because of its structure, situation, and relations, must be regarded as a true post-frontal bone. But this is not to say that it is to be looked upon as an atavistic bone, for unless it can be shown that the factors which determine the appearance of the post-frontal bone in those vertebrates to the skull of which it is normal have determined the separate existence of the bone in this case, it cannot be so regarded. The possibility of such factors having determined the independent development of the post-frontal element in this instance can be completely eliminated and with them the atavistic theory; instead we must look upon the separate existence of this element as a purely developmental anomaly resulting from a failure of union between two normally completely fused bones.

We have already remarked upon the relations of the post-frontal element in Man upon the outer side of the skull. A few observations will now be offered upon the probable contribution of this element to the formation of the orbit in Man.

In Man the relations of the infra-frontal or fused post-frontal differ considerably from those which characterise the gorilla. In Man the alisphenoid occupies the place of the fused post-frontal in the gorilla, which in the latter is wedged between the squamous and the malar for some distance below the fronto-jugal level, whereas in Man the same bone rests upon the alisphenoid and the jugal above that point. We would therefore expect the relations of the said bone within the orbit to differ very appreciably. In Man there is a great increase in the height of the sphenoid within the orbit which assumes more than half the area occupied in our gorilla by the post-frontal element. In Man, therefore, there can be little doubt that the contribution of the post-frontal element to the inner lateral wall of the orbit may be assumed to be the small area situate between the posterior superior half of the malar and the anterior superior two-thirds of the sphenoid, and limited superiorly by the descending margin of the roof.

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THE FORAMEN OF MAGENDIE[1]

By LAMBERT ROGERS

Surgical Unit, The Welsh National School of Medicine

AND C. M. WEST

University College, Cardiff

"What subtle hole is this,

. . . . .

I'll see what hole is here."

Titus Andronicus, Act II, sc. 3.

OBSERVATIONS made when operating in the posterior fossa of the skull, together with dissections of the suboccipital region with the brain and its coverings *in situ*, have enabled us to reach the conclusions herein set forth, regarding the condition of the membranous coverings of the fourth ventricle. We present these conclusions in the hope that they will settle the controversy that has raged around the foramen of Magendie, as to whether this opening is an artefact made by dissection or whether it exists normally. Our object also is to present a description of what we believe to be the normal condition of the lower part of the roof of the human rhombencephalon.

HISTORICAL

On June 16, 1828, in a paper entitled "Mémoire Physiologique sur le Cerveau," read to the Academy of Sciences in Paris, François Magendie (1) of Bordeaux first described in the mid-line of the roof of the fourth ventricle the opening which has since come to be universally known by his name. The openings in the lateral recesses of the fourth ventricle were drawn attention to by Hubert Luschka (3) of Tübingen in 1855, and by Axel Key and Gustaf Retzius (4) of Stockholm in 1875. The discoverers of the lateral foramina believed in the presence of Magendie's opening, Key and Retzius finding it in ninety-eight out of one hundred human brains examined by them and Luschka regarding it as constant in man. The German anatomist, however, believed that in many animals the roof of the ventricle is closed. Prior to Magendie's description, it had evidently been realised that there was some form of communication between the fluid contents of the cerebral ventricles and of the subarachnoid spaces and cisternae, because Bichat (6), Magendie's immediate predecessor in the group of famous French anatomists and physio-

[1] A communication made to the Society of British Neurological Surgeons on November 14, 1930, and to the Anatomical Society of Great Britain and Ireland on November 21, 1930.

logists which also includes Claude Bernard, Cruveilhier and Flourens, believed that, between the veins of Galen in the neighbourhood of the straight sinus, there was an opening which led through the tela choroidea into the third ventricle. Furthermore, in 1847, R. B. Todd (5), Professor of Physiology and General and Morbid Anatomy at King's College, London, stated that he did not believe there was an opening such as Magendie described, but wrote of an endosmosis of cerebro-spinal fluid into the cisterns which he apparently regarded as reservoirs the function of which was to collect the fluid.

In 1826, Burdach (7) had described the hinder end of the fourth ventricle as completely closed (fig. 1 A) and the weight of his authority was such that even after Magendie's careful work and detailed description, many, including some of the most distinguished investigators and leaders of medical thought in the nineteenth century, refused to believe in the median opening. Virchow (8), in 1854, went so far as to deny the existence of any connection between the ventricle and the subarachnoid space, and in 1861, Reichert (9) averred that the foramen is only produced during removal and manipulation of the brain (fig. 1 B). In the same year also, Kölliker (10) stated that there is complete closure of the ventricle in the embryo and that this is the rule in the adult also. In 1896, Cleland and Mackay (11) of Glasgow, in their text-book, wrote of the opening, "It can easily be demonstrated to be artificial, if the dissector be on his guard." Quincke (12), the pioneer of lumbar puncture, in 1872 published a paper from which it is apparent that he regarded Magendie's foramen as very variable and not always demonstrable.

Hess (13) on the other hand examined the problem, using as his material the brains of thirty adults, ten newly born children and seven embryos. In only one instance was he unsuccessful in finding the foramen, and he concluded that it is constant in Man. In 1900 Blake (14) gave the question very careful consideration from the developmental aspect and concluded that in the course of development a bubble-like protrusion of the roof of the fourth ventricle occurs, and that, while in the majority of Mammals the protrusion remains intact, in Man and the Anthropoids rupture occurs, and that in this way the foramen of Magendie is produced[1].

THE CONTROVERSY

The controversy as to the existence of a median aperture cannot yet be considered as settled. Only last year such a distinguished biologist as Sir John Bland-Sutton (15) stated of the opening "that there is no agreement among anatomists in regard to it." In 1923 he had written (16): "This foramen has had such charm for teachers that it maintains a place in text-books, although sealed up by practical anatomists many years ago." To this Prof.

[1] Prof. J. T. Wilson, in a personal communication, writes in support of this suggested method of production of the foramen, and, in a paper, *Journ. Anat.* vol. XL, p. 210, 1906, states: "From the facts and observations detailed in Blake's paper, it seems tolerably well established that the foramen of Magendie, so far from being an artefact, is really the imperfect representative of an epithelial evagination of the cavity of the rhombencephalon."

Wood-Jones (17) had replied: "As a teacher, I fully admit the charm of this foramen, and as a practical anatomist, I also regard it with affection, for of its presence in the undisturbed condition of the roof plate of the fourth ventricle, I have no doubt whatever."

It will be seen that a long-continued and undecided controversy still exists. But to-day it should be possible to decide this controversy, because operations in which the fourth ventricle is exposed are not infrequent, and neurological

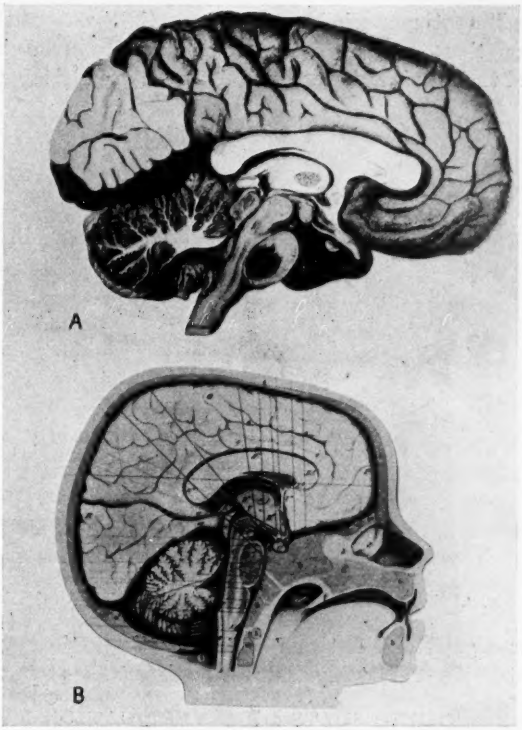

Fig. 1. A, from Burdach, 1819; B, from Reichert, 1861. In each case the fourth ventricle is shown as closed, i.e. there is no foramen of Magendie.

surgeons therefore have opportunities which were denied to their predecessors of noting the condition of the ventricular roof during life. Furthermore, modern cranial instruments have made it possible, with a minimum disturbance of surrounding structures, to open the skull and make accurate and gentle dissection in the cadaver. We have therefore used these two lines of approach to the solution of the problem of what is the actual condition of the coverings of the fourth ventricle during life and after death.

THE PRESENT POSITION

At the present time there may be said to exist two schools of thought regarding the condition of the lower part of the roof of the fourth ventricle, one of which believes it to be completely closed, another which believes in the presence of a median aperture, the foramen of Magendie. Of those who belong to the latter school, a not unusual conception of the opening appears to be that shown in fig. 2 in which it will be seen that the opening is depicted as a small perforation or aperture in the ventricular roof, and indeed it has been so described as "apertura medialis ventriculi quarti." Among those who favour this conception, there also appears to be no unanimity of opinion as regards the position of the opening, some placing it at the apex of the calamus scriptorius, others a good deal farther forward. An inspection of a number of standard text-books of anatomy will substantiate these statements.

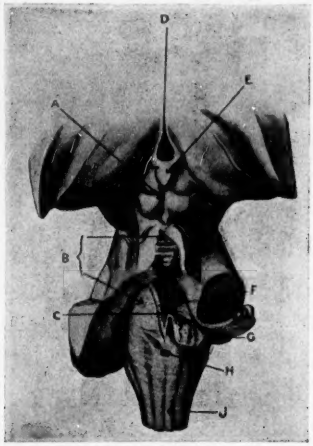

Fig. 2. The foramen of Magendie depicted as a small oval hole.

THE RESULTS OF INVESTIGATION

We believe such conceptions to be both erroneous and misleading.

Our investigations, which have now extended to many specimens, have convinced us that the foramen of Magendie is neither an artefact nor does it exist as popularly conceived, but that normally the whole of the lower part of the rhombencephalon is wide open so that the cavity of the hind brain is in free median communication with that part of the subarachnoid space forming the cisterna magna (figs. 3–6).

If, with the head fully flexed, the dura mater is carefully opened over the lower part of the posterior fossa of the skull, the arachnoidea over the cisterna magna can be preserved intact, and if, as is frequently the case, this mem-

brane is sufficiently transparent, a view into the fourth ventricle can be obtained. When the arachnoid is opened cerebro-spinal fluid escapes, and beneath and between the cerebellar tonsils the naked floor of the ventricle is at once exposed, and a probe can be passed into the ventricle and along its

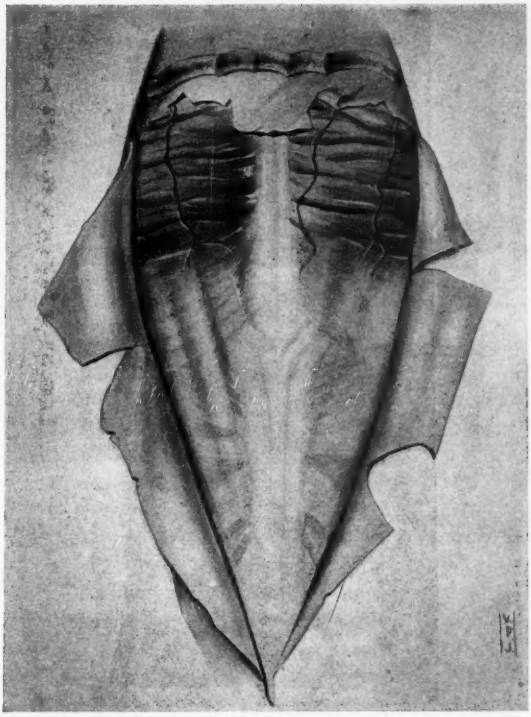

Fig. 3. Drawing of a dissection of the suboccipital region in an adult male. The dura lining the posterior fossa of the skull and covering the upper part of the spinal cord has been opened leaving the arachnoid over the cisterna magna intact.

floor into the Sylvian aqueduct without its traversing any precise aperture in the pia mater, since the only contribution the pia makes to this part of the roof of the ventricle is in the shape of marginal trabeculae passing to the cisternal arachnoid[1].

[1] Since writing this paper we find that W. E. Dandy, in a paper, "The Diagnosis and Treatment of Hydrocephalus due to occlusions of the Foramina of Magendie and Luschka," *Surgery, Gynaecology and Obstetrics*, 1921, p. 112, writes of the three foramina: "These openings are neither myths nor artefacts," and in the same paper: "The foramen of Magendie is exposed at most cerebellar operations and through it the floor of the fourth ventricle is always evident.... I rarely expose the cerebellum without seeing the foramen of Magendie either because it is necessary to look for it or because after the removal of a tumour from this region it is usually brought directly into view."

As the pia mater over the posterior part of the spinal cord is traced upwards, it is found to break up into trabeculae around the calamus scriptorius, while that over the front and sides of the cord is continuous with the pial coverings of the same aspects of the brain stem. A pial sleeve thus surrounds the cord and brain stem, but is defective over the fourth ventricle, the boundaries of the defect being the obex posteriorly and the ligulae posterolaterally. Farther laterally, i.e. outside the ligulae, the pia is continuous with

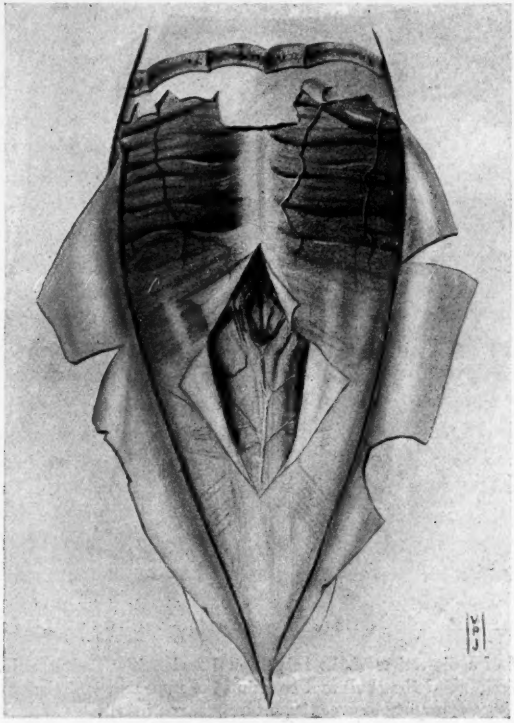

Fig. 4. Same as figure 3, except that the arachnoid has been opened. The cerebellar tonsils can be seen, and below and between them the floor of the fourth ventricle. The foramen of Magendie is a large defect in the lower part of the ventricular roof.

that covering the cerebellar tonsils and the posterior inferior cerebellar artery. The pial sleeve can with ease be dissected back from the ligular edges and the obex, and is not therefore continuous with the ependyma over the ventricular floor. As a rule the pia falls rather short of the ligular margins and may not reach the obex, but in some cases it extends a little above the obex. The boundaries of the roof defect which constitutes the so-called foramen of Magendie are in front, the inferior medullary velum, the degree of develop-

Fig. 5. Photograph of a dissection with brain *in situ*. The lower part of the occipital bone has been removed, also the posterior arch of the atlas. The dura mater has been opened and its cut edges can be seen turned backwards. The arachnoid over the cisterna magna has also been opened and its edges can be seen. The foramen of Magendie is apparent between the two cerebellar tonsils above, and the calamus scriptorius below.

Fig. 6. Photograph of a dissection to show the foramen of Magendie. The cerebellar tonsils are being retracted. The floor of the ventricle is seen. In this case the pia mater over the back of the cord extends slightly above the obex.

ment of which appears to be somewhat variable, behind the obex and the upper trabeculated margin of the pial sleeve, and laterally and behind the ligulae with their associated trabeculated pial coverings. These irregular trabeculated pial margins in all probability represent part of the remains of Blake's bubble ruptured in early intra-uterine life.

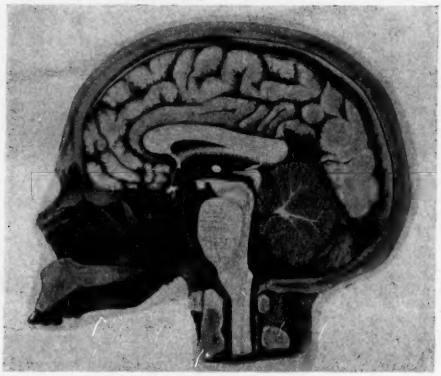

Fig. 7. A sagittal section from Key and Retzius, showing the fourth ventricle in free communication with the cisterna magna. Cf. fig. 1, A and B, in which no communication is shown in either drawing.

The foramen of Magendie is thus a large defect in the roof of the fourth ventricle, through which the ventricle has a wide channel of communication with the cisterna magna covered by its arachnoid (figs. 4, 5 and 6).

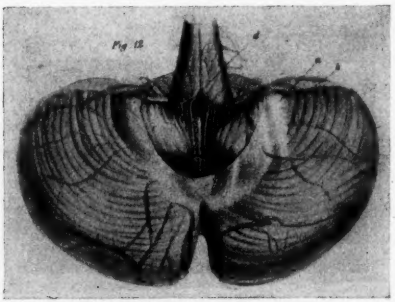

Fig. 8. The foramen of Magendie as depicted by Key and Retzius in *Studien in der Anatomie des Nervensystems und des Bindegewebes.*

In both his *Studies of the Anatomy of the Nervous System* written with Axel Key (figs. 7 and 8), and in his *Das Menschenhirn* (fig. 9), Gustaf Retzius (18) of Stockholm showed an opening such as we describe.

Magendie (2) himself apparently regarded the opening, for which he suggested the term "entrée des cavités du cerveau" or "entrée des ventricules cérébreaux," as variable in size, and believed that this variation depended upon the quantity of cerebro-spinal fluid, for he states,

> Quant à la forme et aux dimensions de l'ouverture, elles sont variables suivant les individus, et suivant la quantité du liquide cérébro-spinal, à tel point que, dans les grandes abondances de ce liquide, l'ouverture peut admettre l'extrémité du doigt.

We believe that normally the entrance to the cerebral ventricles will admit the point of the little finger, and thus summarise our conclusions as to the condition in the normal adult:

1. There is no roof plate to the lower part of the fourth ventricle, but this cavity is freely open to the cisterna magna and is here only covered in by the cerebellar tonsils.

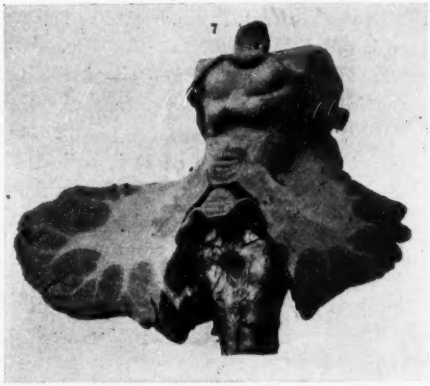

Fig. 9. An illustration from *Das Menschenhirn* (Retzius), showing the foramen of Magendie as a diamond-shaped opening.

2. The upper part of the lower half of the ventricle is closed above by the inferior medullary velum which varies somewhat in extent, but is usually narrow and makes a relatively small covering.

3. There is no relatively small and roughly circular, median aperture, as is frequently depicted and regarded as the foramen of Magendie.

4. The roof defect is somewhat pentagonal in outline and irregular at its edges which are fringed with pia-arachnoid trabeculae, probably remnants of Blake's bubble.

5. The opening extends roughly from the inferior medullary velum above to the obex below and to the ligulae laterally as the trabeculated pial margins approximate very closely to these boundaries.

6. Certain illustrations depicting the foramen as a small median aperture

varying in position between the apex of the calamus and the middle of the ventricular roof may be examples of adhesive leptomeningitis[1].

7. When, with the head fully flexed, the arachnoid over the cisterna magna is opened the floor of the naked fourth ventricle becomes apparent, and is rendered more so when the cerebellar tonsils are gently separated.

8. Magendie's foramen should be looked upon, not as an opening in, but as a complete defect of the lower part of the roof of the fourth ventricle. His description of the opening, as the entrance to the cerebral ventricles, capable in some cases of admitting the point of the finger, is more accurate than that given by certain anatomists since his day.

SUMMARY

1. Observations of the calamus region of the human bulb have been made in the living when operations were being carried out in this region of the brain, and also in cadavers.

2. A brief history of the controversy concerning the presence or absence of Magendie's foramen is given.

3. Evidence is produced to show that among those who believe in Magendie's foramen, a false conception exists as to the nature, the size and the position of the opening.

4. Conclusions are set forth showing what is believed to be the normal condition in the human adult, namely an opening which, instead of being a median aperture, is a complete defect in the lower part of the ventricular roof through which the ventricle is in free communication with the cisterna magna.

5. The position and relations of the roof defect are given, and its appearance is illustrated.

We are indebted to the Medical Research Council for defraying the expenses of this investigation.

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[1] In a personal communication Mr Norman Dott, of Edinburgh, writes in this connection: "I have twice seen in cases of chronic peri-cerebellar leptomeningitis a well-defined small aperture in the thickened scar tissue covering the roof of the fourth ventricle from which cerebro-spinal fluid escaped in a very definite stream."

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A METHOD OF STAINING THE BRAIN FOR MACROSCOPIC STUDY

By JOHN H. MULLIGAN, M.B., Ch.B. (Aberd.)

Anatomical Laboratory, St Thomas's Hospital Medical School

In 1926 Sincke described a method of staining sections of brain hardened in formalin and intended for naked-eye examination. Briefly stated this method consisted in placing the sections first in an aqueous solution of iron chloride and then, after washing, in an aqueous solution of potassium ferrocyanide. The grey matter in specimens treated in this way was stained a dark blue and the white matter a very pale blue.

Two years later Mainland published the results of an investigation which he had made of this procedure, and gave details of his discovery of a method of making the specimens more permanent.

In the early summer of 1930 Prof. Le Gros Clark observed patches on the white matter of sections stained by Sincke's method which, instead of being pale blue, were almost perfectly white. He pointed out that these patches were confined to the white matter, and that, should the cause of this be discovered, a method might be devised by which all the white matter could be left unstained, thus giving a marked contrast with the stained grey matter.

It was thought that, during the cutting of the sections, the lipoids of the myelin sheaths in the unstained patches had been smeared over the adjacent brain by the knife, and that they had protected the axis-cylinders and neuroglia from the action of the staining reagents. The problem, therefore, arose as to how this effect could be produced over the entire surface of the exposed white matter. A fat solvent naturally suggested itself as an agent which might be used to attain this end, for the lipoids of a section of brain placed in such a solvent might, in the process of dissolving, be spread over the neighbouring axis-cylinders and neuroglia.

A brief account of the work done along these lines will be given under three headings: (1) the preparation of the brain, (2) the stain used in colouring the grey matter, and (3) the formation of the protective film.

(1) THE PREPARATION OF THE BRAIN

It was found important that the brain should be as free from blood as possible, for the blood pigment stained the cut surface of the white matter and spoiled the contrast between the white and grey matter in the finished specimens.

The brain was thoroughly hardened in Kaiserling. Sections were then cut with a very sharp knife, and these were washed overnight in running tap water. They were then refixed for at least eight hours in 10 per cent. formalin. They were washed again for twelve hours in running tap water, and were finally placed in distilled water for one hour in order to remove the alkaline salts found in tap water. It seemed to be very desirable to have perfect fixation of the specimens, and the refixation of the cut surface greatly improved the depth of staining of the grey matter (Plate I, figs. 1 and 2).

(2) THE STAIN USED IN COLOURING THE GREY MATTER

Sincke's method of staining was tried, but it was discarded because a more marked contrast could be obtained by the use of tannic acid and an iron salt. This stain is used by histologists, and was described by Lennhoff (1910).

For the purpose of the method given in this paper the specimens were placed first in 2 per cent. tannic acid dissolved in distilled water. They were then washed and placed in 2 per cent. iron alum in the form of the violet crystals dissolved in distilled water. The tannic acid first combined with the protein, and later formed an intensely black compound with the iron. The solutions of both reagents were used soon after being made.

(3) THE FORMATION OF THE PROTECTIVE FILM

In order to be successful the protective film must cover the white matter completely, and yet leave the grey matter wholly uncovered. It must also be impermeable to the staining reagents.

Chloroform, carbon tetrachloride, xylol and carbolic acid were investigated as regards their value in forming such a film with the lipoids of the myelin sheaths. Of these chloroform and carbon tetrachloride were unsatisfactory, and carbolic acid was found to be the most efficient and the least expensive. Xylol gave moderately good results, and a great many methods were planned involving its use. It may be of interest to outline some of these prior to describing the carbolic acid method.

A. Xylol methods

Since xylol is very insoluble in water, the presence of water on the surface of the white matter tended to prevent the xylol dissolving in the lipoids. Therefore, when specimens were placed in xylol, the film formed was incomplete, and the stained surface showed blotching of the white matter. On the other hand, when the surface of the brain was dried with filter paper or alcohol, the xylol tended to adhere to the grey matter which appeared mottled after being stained.

Four of the methods used in an attempt to overcome this difficulty will be mentioned.

(*a*) Emulsions of xylol and water made with soap were applied to the surface of the sections. This did not prevent the blotching.

(β) The surface of the brain was dried with filter paper and exposed to pure xylol. The film formed was differentiated with 10 per cent. alcohol which detached the xylol from grey matter. The differentiation was difficult to control, for the film tended to be detached from the white matter as well.

(γ) Several of the higher grades of alcohol saturated with xylol were applied to the sections. The film formed consisted partly of alcohol and was permeable to tannic acid, since tannic acid is soluble in alcohol.

(δ) The specimens were first washed in 2·5 per cent. sodium chloride in distilled water, and were then transferred to 60 per cent. alcohol saturated with xylol. The sodium chloride on the surface of the section led to the salting out of the alcohol and thus of the xylol, and a film of relatively pure xylol was deposited on the white matter. This was the best of the xylol methods, but was very uncertain in its working since the salt carried over with the specimens soon precipitated the xylol from the mixture of xylol and alcohol and rendered it useless.

B. Carbolic acid method

Carbolic acid was first used as an aqueous solution in conjunction with xylol in the hope that it would help in the application of the xylol film to the brain by enabling the xylol to wet the surface of the brain. It was used because it was known to be soluble both in water and xylol and to have a pharmacological effect on nerve tissue. The experiment was a failure in that it led to a filming over of the entire surface of the brain.

This experiment was, however, repeated as the result of a conversation with Prof. R. H. A. Plimmer concerning the removal of alcohol from alcohol-xylol films, which he suggested might be done by the use of carbolic acid. On this occasion the proportion of xylol was varied, and it was found that the less xylol used the better was the differentiation. In fact without xylol the carbolic acid produced a moderately satisfactory film.

Xylol was then discarded as an agent for producing the film since carbolic acid gave good promise of producing better results with greater certainty, and investigations were carried out in order to discover the best manner of using carbolic acid.

It was found that the addition of a trace of mineral acid to the carbolic acid solution helped greatly in the formation of the film. The desired effect was obtained with $\frac{1}{8}$ per cent. concentrated hydrochloric acid.

Heating the carbolic acid solution gave a great improvement and a temperature of 60° C. was found to be the best.

Excellently differentiated films were obtained by placing the specimens in 4 per cent. carbolic acid and $\frac{1}{8}$ per cent. concentrated hydrochloric acid at a temperature of 60° C. for two minutes. Higher concentrations of carbolic acid and longer periods in the solution made the subsequent staining less intensely black.

Unfortunately within twenty-four hours, as the specimens were being washed and as the films wore off, it was found that the subjacent white matter was stained. The films were thus seen to be permeable to tannic acid.

This was probably in part due to the contracting of the hot carbolic acid solution in the interstices of the brain tissue and in the small vessels when the specimens were put in the cold tannic acid solution. Such a contraction must have led to a drawing of the tannic acid solution into the depths of the brain section below the film and thus produced staining of the white matter. By placing the specimens in cold water before transferring them to the tannic acid solution the staining of the white matter was greatly diminished.

The addition of $\frac{1}{2}$ per cent. crystalline copper sulphate ($CuSO_4$, $5H_2O$) to the tannic acid solution rendered the film highly impermeable when used in conjunction with the cold water as described above. The copper sulphate was added with a view to precipitating the tannic acid on the surface of the carbolic acid and lipoid film in the form of an insoluble copper tannate. This reaction was probably assisted by the use of the cold tap water which is slightly alkaline and thus prevented the dissolving of the copper tannate by the acid in the film.

An outline of the method involving the use of carbolic acid is given here for the purpose of reference.

(1) Fix the brain very thoroughly in Kaiserling or formalin.

(2) Cut it in slices with a sharp knife and wash these for twelve hours in running water.

(3) Refix the slices in 10 per cent. formalin for eight hours.

(4) Wash in running water for twelve hours and in distilled water for one hour.

(5) Place in the following mixture at a temperature of 60° C. for two minutes:

4 per cent. carbolic acid (crystalline),

$\frac{1}{2}$ per cent. copper sulphate (crystalline), and

$\frac{1}{8}$ per cent. concentrated hydrochloric acid dissolved in distilled water.

The hydrochloric acid should be measured carefully. At least two litres of the solution should be prepared, and it should cover the sections to a depth of at least one-and-a-half inches. It may be heated in an enamelled metal basin with an intact enamel.

(6) Place in a large volume of cold water for one minute.

(7) Place in 2 per cent. tannic acid dissolved in distilled water for one minute.

(8) Wash in running tap water for five minutes.

(9) Place in 2 per cent. iron alum in distilled water till the grey matter is black.

(10) Wash in running tap water for twenty-four hours.

(11) Cover a sheet of glass with a thin layer of 20 per cent. gelatin dissolved in distilled water and rendered fluid by heating. Place the specimen on the

gelatin, and allow it to become fixed in position in the cold. Then cover the specimen with a thin layer of gelatin, and allow this also to set in the cold. Harden the gelatin in 10 per cent. formalin for half an hour. Preserve the preparation in 70 per cent. alcohol.

I desire to thank Prof. R. H. A. Plimmer and Mr J. Lowndes for their help and expert advice. Finally I wish to acknowledge again that Prof. Le Gros Clark pointed out the possibility of such a method as that described and to thank him for daily encouragement in the search for it.

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EXPLANATION OF PLATE I

Fig. 1. Untouched photograph of a sagittal section of the human brain. The specimen was stained by the carbolic acid method prior to refixation in 10 per cent. formalin.

Fig 2. Untouched photograph of a coronal section of the human brain passing through the lateral geniculate bodies. The specimen was stained by means of the carbolic acid method after refixation in 10 per cent. formalin.

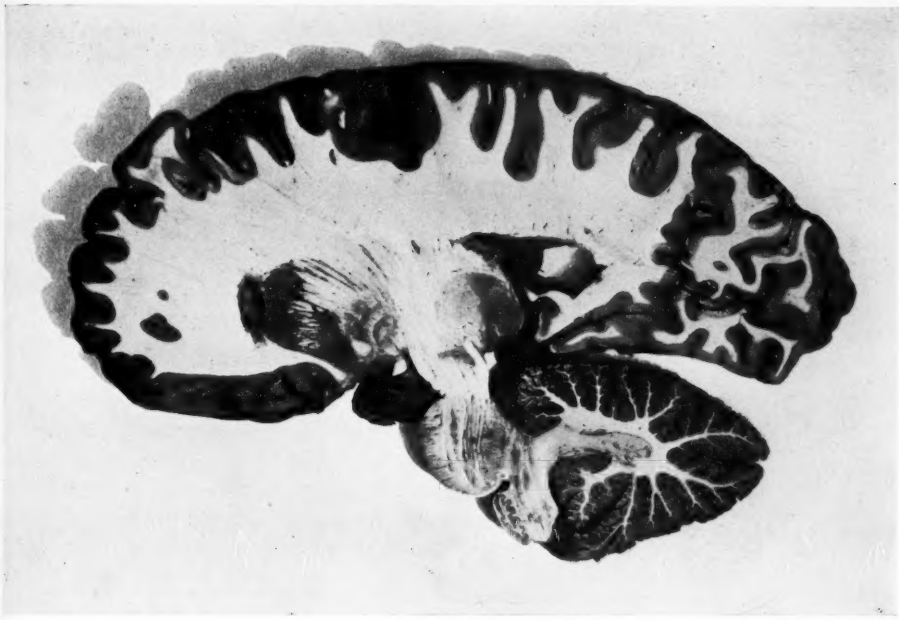

Fig. 1

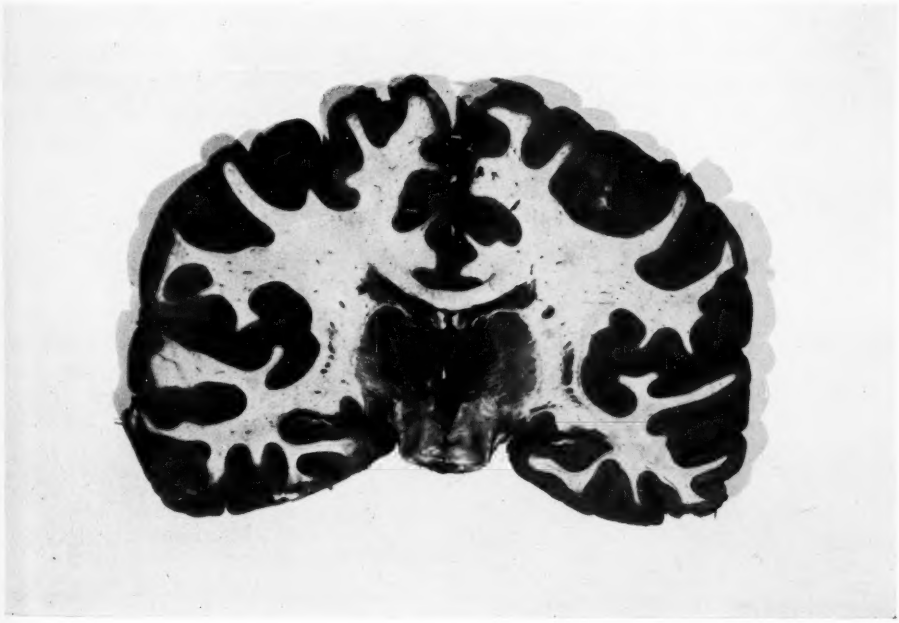

Fig. 2

THE CAPSULE AND TRABECULAE OF THE SPLEENS OF DOMESTIC MAMMALS

By J. TEHVER, Dr med. vet.
and T. GRAHAME, F.R.C.V.S.

Anatomy Department of the Royal (Dick) Veterinary College, Edinburgh.

INTRODUCTION

The main parts of the spleen, the variations of which cause characteristic features in the different species of domestic Mammals, are the capsule and the trabeculae. Statements concerning these structures in the various species nevertheless are almost entirely lacking in the standard text-books on veterinary anatomy (Ellenberger and Baum (1), Martin (3), Sisson (4)) and histology (Ellenberger (5), Ellenberger and Trautmann (2)).

The purpose of the present paper therefore is to indicate shortly these macroscopic and microscopic variations; but a description of the finer histological differences is omitted.

MATERIAL AND TECHNIQUE

The material used for macroscopic and microscopic investigation was taken from the spleens of five horses, five oxen, five sheep, five pigs, four dogs and one cat. The fixing fluids were 10 per cent. formol, absolute alcohol and susa fixative. The last named seemed to produce the least amount of shrinkage. To avoid distortion of the capsule and trabeculae the complete organ or very large pieces were fixed. Single and serial sections from 10 to 20 microns were made.

Haematoxylin (without a counterstain) proved to be the most useful stain to distinguish the capsule and trabeculae from the pulp. For the histological investigation Kull's[1] copper-carmine with indigo-carmine, van Gieson's stain and Weigert's resorcin-fuchsin were used. Kull's copper-carmine with indigo-carmine is especially recommended for the differentiation of the various struc-

[1] Kull's copper-carmine (*Eesti arst* Nr. 11/12, 1923, Estonian): cupr. acet. neutr. cryst. 2·0; carmine (Merck or Gruebler) 2·0; aq. dest. 100 c.c. (stock solution).

As much of the stock solution as is required is taken and ammonia added until all the carmine passes into solution, which is indicated by a clearing of the solution (Petri dish may be used). The section is stained from 20 to 60 min. and then differentiated in acid alcohol (5–10 drops of conc. HCl in 100 c.c. of 70 per cent. alcohol).

Counterstain with Calleja's picro-indigo-carmine (indigo-carmine 1·0; picric acid, conc. aq. sol. 400 c.c.). Stain for a few minutes.

The method has been slightly modified by using heat (as in Altmann-Kull staining). Gurr's carmine, used by us, did not go perfectly into solution, but this did not affect in any way its staining property.

tures of the spleen, as each is clearly defined by a distinct colour: peritoneum (connective tissue)—blue; capsule and trabeculae (muscular tissue)—greenish yellow; pulp—light red; Malpighian corpuscles—dark red; nerve fibres are very faintly stained. By this method also the connection of the blood vessels with the trabeculae is clearly shown.

For the gross study of the capsule and trabeculae specimens were macerated and thoroughly washed in water. From the spleens of animals in which the trabeculae are very strong and coarse (Horse and Ruminants) the pulp may be washed in the fresh state; but in all animals it is much easier to wash out the pulp after maceration. For that purpose the spleens were kept in water at room temperature for 3–6 days, and transverse sections 1 cm. in thickness were then cut and washed. The process is expedited by gently squeezing the sections between the fingers under a stream of water. This method is only advised for Horse and Ruminants' spleens. To wash the pulp from the spleens of the smaller animals the sections were fixed to a cork plate with pins. During the process of washing the pieces appear to lose their shape, but this is regained when they are placed in water or fixing fluid. Strong formol solution (20 per cent.) is recommended for hardening and keeping such specimens.

From the spleen of the pig alone were we unable to wash out the pulp satisfactorily.

In Ruminants (in contrast to all other domestic Mammals) it is possible to make the trabeculae more distinct by taking away the arteries; these being so loosely attached to the trabeculae that their removal may be effected without injury to the trabecular tissue. It is better to do this after fixation, for, if done before, there will be shrinkage due to absence of support.

The photographs used in the illustrations were all taken from specimens prepared according to the foregoing method.

MACROSCOPIC CHARACTERS OF THE CAPSULE

The outer covering (capsule) of the spleen consists of two parts: (1) an inner muscular layer (capsule proper), and (2) peritoneal coat with a subperitoneal layer. In Ruminants the dorso-cranial part of the spleen is devoid of peritoneum and here the proper capsule is covered by adventitious tissue.

The colour of the organ varies according to the thickness of the capsule. The spleen has a grey tinge in the ox and the horse, a pink tinge in the pig and a brownish colour in Carnivora. A marbled (pig) or dotted (dog) appearance of the surface of the spleen depends upon the attachment of the trabeculae to the translucent capsule. When, in Carnivora, splenic (Malpighian) corpuscles occur near the surface, their presence may be occasionally determined, contributing to the dotted appearance.

In colour the capsule of the spleen of the sheep is intermediate between that of the ox and pig. The dorso-cranial surface is grey and like that of the ox, while the ventro-caudal surface is pink and similar to that of the pig.

Contrary to the statement made by Tellyesniczky (5), the two layers of the

capsule in the Ruminants (and even in the horse) are loosely attached to one another and may be readily separated. In pig and Carnivora separation by dissection is impossible since the layers are very thin and firmly attached to each other.

The peritoneal coat of the horse's spleen is more or less equally thick throughout, except the very periphery, where it is thinner. It is about the same thickness as the capsule proper. In Ruminants the peritoneal coat is thinner than it is in the horse, and thinner than the capsule proper. In the spleen of the sheep it is particularly thin in the caudo-ventral part of the organ.

The separation of the capsule proper from the parenchyma is easily carried out in the spleens of all animals when the organ has been fixed, but in the unfixed specimen the process is almost impossible. The closest adhesion of capsule to parenchyma is observed in the horse's spleen.

The inner surface of the detached capsule varies characteristically in the different species. This variation is due to the appearance of the inner surface of the capsule itself and to the form, size and closeness of the origins of trabeculae.

The areas between the attachments of the trabeculae to the deep face of the capsule are more or less flat in all animals except the horse, whose areas are represented by small impressions or fossae, which, when the capsule is removed, remain filled with splenic tissue (Plate I, fig. 6).

The attachments of the trabeculae to the capsule are commonly rounded, but sometimes flattened. The base of attachment is narrow in Carnivora and Ruminants, but in the horse it broadens out to form a cone-shaped origin (Plate II, fig. 1). The diameter of the attachments of the trabeculae is least in Carnivora, greater in the sheep, still greater in the ox and reaches its maximum in the horse. In the horse, moreover, the diameter is more or less constant throughout the organ, but in the other animals there is considerable variation in different parts.

The pig differs from the other animals inasmuch as the inner surface of the capsule has a honeycomb appearance; the bases of the trabeculae coalescing and forming irregular low ridges (Plate I, fig. 9). This is the cause of the marbled appearance of the outer surface of the organ, as mentioned above.

The number of the trabecular attachments to square centimetre of capsule is about 75–100 in the horse, 20–50 in the ox, 40–80 in the sheep and about 500 in Carnivora.

In hardened specimens from which the capsule has been dissected, the origin of the trabeculae may be easily studied by observation of the surface of the hardened parenchyma.

The peculiarities of the structure of the capsule already mentioned influence greatly the picture presented by sections; and it seems that the appearance of the capsule in sections is more characteristic than its thickness.

In the horse the thickness of the capsule is inconstant, a variation that may

be demonstrated even in a single section of only about 1 cm. in length (Plate II, fig. 1). The cone-like attachment of the trabeculae is apparently correlated with an increase in their number. The wavy appearance of the inner surface of the capsule of the pig, produced by the ridges mentioned above, is as characteristic as the ridges themselves (Plate II, fig. 1). In the Carnivora the capsule is very thin and uniform throughout.

MICROSCOPIC CHARACTERS OF THE CAPSULE

In the larger animals (Horse and Ruminants) the splenic capsule is divisible histologically into two definite coats: outer peritoneal and inner muscular. The peritoneal coat with its sub-peritoneal layer consists of fibrous connective tissue without muscle fibres, and is abundantly supplied with vessels. The capsule proper consists of plain muscle fibres with a very scanty admixture of fibrous tissue. The direction of the muscle fibres varies, but definite strata may frequently be distinguished. The line of demarcation between the peritoneal layer and the muscular capsule is a sharp one, though some connective tissue fibres of the sub-peritoneal tissue may insinuate themselves into the muscular capsule, thus forming a supporting framework. Kull-Calleja's staining method demonstrates both strata most clearly as indicated by Plate I, fig. 11.

Elastic fibres, which are found throughout the capsule, are denser in the deeper part; but they are not absent in the peritoneal coat, as Tellyesniczky's (5) fig. 209 would appear to indicate (Plate I, fig. 10). In the capsule proper they run parallel to the muscle fibres.

In the pig and Carnivora the distinction between the peritoneum and capsule proper is not so clear, and a much greater amount of connective tissue penetrates the muscular coat. In these animals the elastic tissue is just as abundant as in the larger animals, but the fibres are thinner and in the Carnivora they form a reticulum.

The thickest peritoneal coat occurs in the horse, where it forms about half of the capsule (see the white demarcation lines in Plate II, fig. 1). The peritoneum of the ox constitutes about one-third of the capsule; then follow in diminishing ratio the sheep, the pig and the Carnivora.

The thickness of the capsule in microns is as follows: horse 100–420–500; ox about 400; sheep about 250; pig 50–125–165; Carnivora about 50. The middle numbers in the horse and the pig indicate the average thickness.

MACROSCOPIC STRUCTURE OF THE TRABECULAE

Reconstruction models were made of part of the spleen of several animals, but the method was found to be not entirely satisfactory. Even when dealing with the organs of the smaller animals, it is only practicable to model a very small proportion of the whole spleen, with the result that a false impression may be obtained of the general disposition, etc., of the trabeculae. It was found

that the most convenient and accurate method was the study of organs from which the pulp had been thoroughly washed.

As shown in Plate I, fig. 1, the trabeculae of the horse's spleen are regularly distributed throughout. They are thick and rounded, and branched and joined in such a manner as to form an intricate and involved meshwork. The meshes of the reticulum are rounded and vary in diameter. The network itself is so firmly connected with the larger vessels that it is torn when a vessel is pulled away.

The distribution of the trabeculae in the spleen of Ruminants is very irregular. They are mostly rounded, but occasionally flattened, and arranged in a direction at right angles to the capsule. In the thinner parts of the spleen they run directly across the organ, and are attached to the capsule on the opposite side (Plate I, figs. 2 and 3). The trabeculae in the centre of the spleen are stronger and much thicker than those of the periphery. The interstices between the trabeculae are elongated and variable in size. The loose connection between the vascular system and the trabeculae has already been mentioned. The adventitia of the artery may be connected with the trabeculae, but such a connection is only of rare occurrence. The larger arteries are surrounded by fine filamentous trabeculae (Plate I, fig. 8).

The trabeculae of the spleen of the pig are fine, rounded, often flattened (especially at the edges of the organ), much branched and closely connected with the vessels.

Besides the macroscopic trabeculae in the spleens of the Ruminants and the pig there are others, which, consisting of a single or few muscle fibres, can only be distinguished under the microscope. Their great number and close connection with the larger trabeculae in the pig's spleen hinder the washing out of the pulp. A detailed description of them is here omitted.

In the Carnivora the arrangement of the trabeculae resembles that of the horse, but their form and diameter vary greatly (Plate I, fig. 4).

MICROSCOPIC STRUCTURE OF THE TRABECULAE

Since they consist of muscle fibres with some amount of fibro-elastic tissue the histological structure of the trabeculae in all domestic animals is similar to that of the capsule proper. The course of the muscle and connective tissue fibres is parallel to that of the trabeculae. Their structure does not offer any characteristic difference of moment.

The appearance of the trabeculae in the macroscopic and microscopic sections of the spleen are indicated in Table II (see also Plate II, fig. 2, Plate I, fig. 4).

Besides the form, size and structure of the trabeculae and their connection with the blood vessels, there is a certain degree of variation in the ratio of the volume of the trabeculae to that of the pulp. For the determination of this both direct and indirect methods may be employed. The direct way appears to be more accurate, but it is not applicable to every animal (the pig, for

example), and furthermore, the amount of water that remains between the trabeculae after washing cannot be regulated in any way. Inaccuracy in the indirect method results from the various processes of manipulation required (drawing, cutting, uneven thickness of the paper, smallness of the pieces, etc.). In consequence of these possible fallacies one can expect only approximately correct results from either method.

In the use of direct method, pieces from macerated spleens were cut and their volume measured by water displacement in a graduated cylinder. The pieces were then washed, the water pressed out, and the volume again deter-

Table I. *The ratio of the volume of trabeculae to that of the pulp.*

Animal	No. of the piece used	Weight of the trabeculae in gm.	Weight of the pulp in gm.	Ratio
Horse 1	2	7·125	31·625	1 : 4·44
2	2	6·250	24·600	1 : 3·94
2	7	11·850	51·325	1 : 4·33
4	2	4·425	18·800	1 : 4·25
5	2	4·900	14·725	1 : 3·01
Totals	...	34·550	141·075	1 : 4·08
Ox 1	2	0·450	20·750	1 : 46·11
1	5	1·275	43·250	1 : 33·92
2	2	0·700	23·825	1 : 34·04
3	2	2·225	39·075	1 : 17·56
4	2	1·450	40·650	1 : 28·03
Totals	...	6·100	167·550	1 : 27·47
Sheep 1	2	1·350	26·100	1 : 19·33
2	2	2·475	35·125	1 : 14·19
2	5	3·075	43·525	1 : 14·15
4	2	5·775	56·025	1 : 9·70
5	2	1·950	37·725	1 : 19·86
Totals	...	14·625	198·500	1 : 13·57
Pig 1	2	0·450	12·150	1 : 27·00
1	5	4·350	45·675	1 : 10·50
3	2	1·950	36·825	1 : 18·88
4	2	1·850	41·800	1 : 22·59
5	2	1·825	33·725	1 : 18·48
Totals	...	10·425	170·175	1 : 16·32
Dog 1	—	2·325	14·300	1 : 6·15
1	—	1·075	5·100	1 : 4·74
Totals	...	3·400	19·400	1 : 4·41

mined. The results thus obtained for the ratio of the volume of the trabeculae to the pulp in the different species are as follows: horse 1 : 3, 5; ox 1 : 13; sheep 1 : 10; dog 1 : 5. These ratios are quite uniform in one and the same species, and more in favour of the trabeculae than in Table I.

The results tabulated in Table I have been obtained by the following indirect method. From serial sections 20 microns thick drawings were made by means of an Abb drawing apparatus. The magnification used was 25 diameters. The paper was of more or less even thickness. The outlines of the trabeculae were then separated from the pulp by cutting and then weighed.

Table II

Animal	Colour of the surface of the organ	Superficial marking	Detachment of the peritoneum from the capsule proper	Ratio of the thickness of peritoneum to that of the capsule proper	Inner surface of the capsule	Attachments of the trabeculae to the capsule	Capsule in transverse section	Thickness of the capsule	Number of attachments of trabeculae to the capsule per 1 sq. cm.	Trabeculae in washed specimen	Trabeculae in sections	Ratio of the volume of trabeculae to that of the pulp in sections
Horse	Greyish	None	Possible	1 : 2	Regular rounded depressions present	Cone-like	Uneven thickness in a single section	ca. 420 μ	70–100	Rounded. Of equal thickness throughout. Regular distribution. Form rounded spaces. Firmly connected with the blood vessels	Marble-like. This picture is independent of the direction of the cut	1 : 4
Ox	Greyish	None	Possible	1 : 3	Even	Narrow	Equal thickness	ca. 400 μ	20–50	Rounded, sometimes flattened. Unequal thickness. Run at right angles to the surface. Elongated spaces. Loose connection with the blood vessels	In transverse sections only few trabeculae, cut lengthwise, are to be seen. In longitudinal sections they are cut across and scarcely visible	Varies (1 : 27)
Sheep	Dorso-cranial part greyish, caudo-ventral reddish	None	Possible	1 : 4–5	Even	Narrow	Equal thickness	ca. 250 μ	50–70	As in the ox	As in the ox	Varies (1 : 13)
Pig	Pinkish	Marbled	Impossible	—	Honeycomb-like ridges	By means of ridges	Inner surface wavy	ca. 120 μ	—	The general distribution as in Ruminants. Both rounded and flattened trabeculae are present	In general like those of the Ruminants. Otherwise scarcely visible at all	Varies (1 : 18)
Dog and cat	Brownish	None or finely spotted	Impossible	—	Even	Narrow	Equal thickness	ca. 30–50 μ	ca. 500	The distribution as in horse, but not so regular. More variation in the thickness of trabeculae than in other domestic Mammals	The direction, form and thickness of the trabeculae vary in every section. Almost all large trabeculae contain veins	1 : 6

The extraordinarily wide deviations of these ratios in the ox, and also in lesser degree in the sheep and the pig, are explained by the irregular distribution of the trabeculae in these animals (see Plate I, fig. 7). By comparison, the ratios in the horse are practically constant.

From these data, which are scarcely sufficient to distinguish the spleens of the various species, we may conclude: (1) That the spleen of the horse possesses the largest quantity of trabecular tissue. In descending order come the Carnivora, sheep, pig and ox (the microscopic trabeculae are not here taken into account). (2) That one can scarcely employ the ratios obtained by the indirect method to distinguish the spleens of the ox, sheep and pig from one another. (3) That the varying results conform closely with the description of the trabeculae given above.

The differences observed are summarised in Table II.

ACKNOWLEDGMENTS

The authors gratefully acknowledge their indebtedness to Dr O. Charnock Bradley, Principal of the Royal (Dick) Veterinary College, Edinburgh, for suggesting the theme and for his advice. Also to Drnd. med. vet. G. Tehver for assistance in making the reconstruction models and composing Table I.

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EXPLANATION OF PLATES I AND II

Plate I

Figs. 1, 2, 3 and 4. Transverse sections of the washed spleens of the horse, ox, sheep and dog respectively. Photograph × 0·5. In the ox and partly in the sheep the blood vessels are removed.

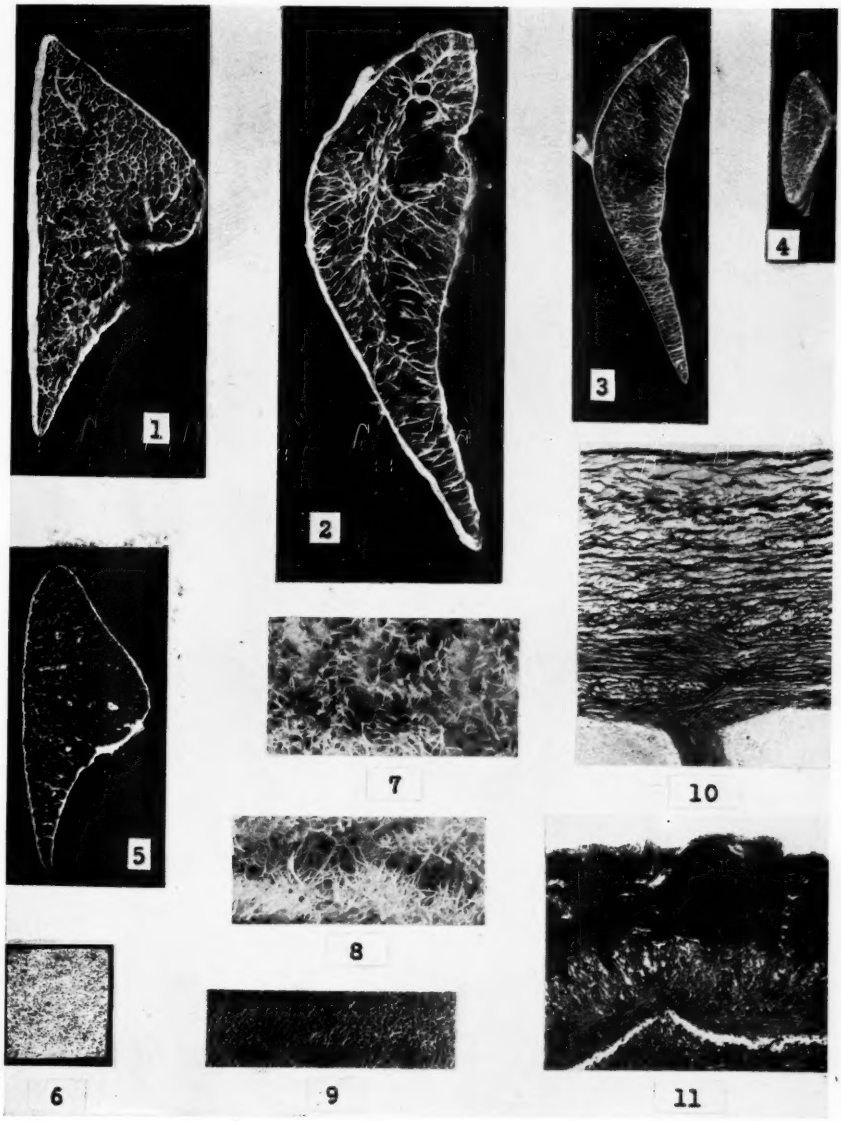
Fig. 5. Section from the fixed spleen of the horse showing the great amount of trabecular tissue. The appearance of the trabeculae in sections does not depend upon the direction of the section. Photograph × 0·5.

Fig. 6. Inner surface of the capsule of a foal's spleen. Numerous tiny depressions filled with the splenic tissue are black. Photograph × 0·5.

Fig. 7. Irregular attachments of the trabeculae to the inner surface of the ox spleen. Large areas without any trabeculae are seen. Photograph × 1.

Fig. 8. Marked depression between the trabeculae after pulling away the corresponding artery. Around the artery are only very fine trabeculae. Ox. Photograph × 1.

Fig. 9. Honeycomb-like ridges on the inner surface of the pig's spleen. Photograph × 0·5.



Figs. 1–11

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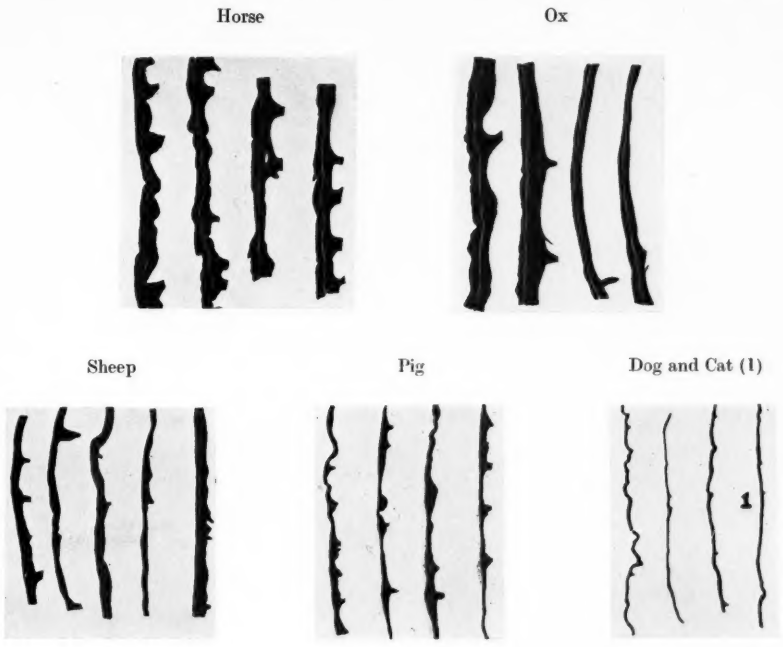

Fig. 1

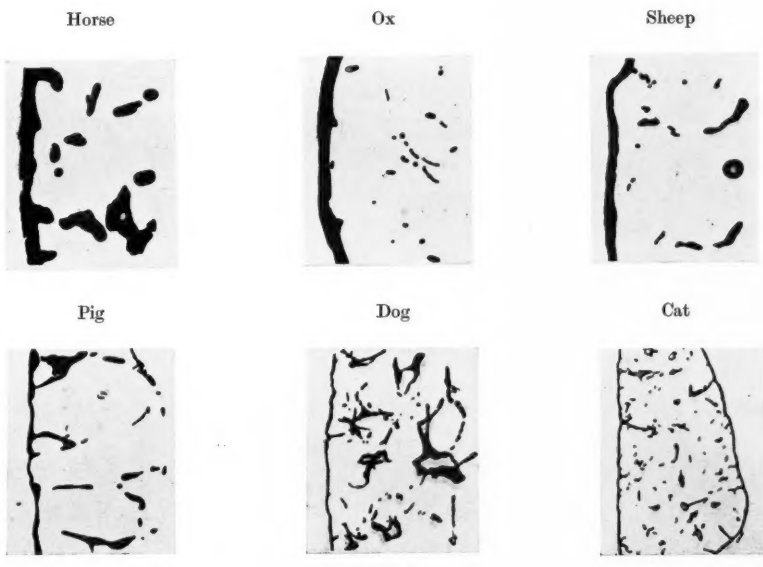

Fig. 2

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Fig. 10. Capsule of the ox spleen showing the elastic tissue. This is denser in the deeper part of the capsule (below), but it is not absent in the peritoneal part (above). Fixative: 10 per cent. formol; stain: Weigert's resorcin-fuchsin. Microphotograph × 65.

Fig. 11. Capsule of the horse's spleen. The peritoneal (darker) and the muscular (lighter) coats are markedly separated by different colours (in the slide the darker part corresponds to the blue and the lighter to the greenish-yellow). Both are of about the same thickness. The white line indicates the boundary between the capsule and the pulp. Fixative: 10 per cent. formol; stain: Kull-Calleja. Microphotograph × 60.

PLATE II

Fig. 1. Transverse sections of the spleen capsule of domestic mammals. Drawings × 5. Each drawing was made from a different individual.

Fig. 2. Appearance of the capsule and trabeculae of the spleen in microscopic sections. Drawings × 5.

A REPORT ON THE SPINOUS PROCESSES OF THE CERVICAL VERTEBRAE IN THE NATIVE RACES OF SOUTH AFRICA

By L. R. SHORE, M.A., M.B., M.R.C.P., D.P.H.
University of the Witwatersrand, Johannesburg, South Africa

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I. INTRODUCTION

It is remarkable that, despite their importance in the interpretation of primitive human remains, so little precise information is available concerning the spinous processes of the cervical vertebrae of the living races of mankind. In this place it will suffice to recall the well-known facts that the cervical spinous processes of living anthropoids are not bifid, and that those of the human species are regarded as bifid.

It has been stated by Boule (1) that Neanderthal Man resembles the ape in having non-bifid cervical spinous processes. Referring to the fossil human skeleton from La Chapelle-aux-Saints, he writes: "their spinous processes are long...and they are not bifurcated at the end."

Duckworth (2) also compares the cervical spinous processes of Neanderthal Man with those of modern Man and of gorilla in his account of the last, "these spinous processes are not, however, bifid, and thus differ from those of existing human races of Europe, although approached in this respect by the cervical vertebrae of the primitive human races in other regions, and also the historic skeleton from La Chapelle-aux-Saints in France."

It is true that the European cervical spinous processes have been intimately described, and that some minor observations have been made concerning the conditions found in other races, but seldom on an extended series of any one race. Thus Morris (3) writes: "as a rule, among Europeans, the second, third,

fourth and fifth vertebrae possesses bifid spines...sometimes the sixth has a bifid spine, and, more rarely, the seventh presents the same condition....In the lower races of Man the cervical spines are relatively shorter and more stunted than in Europeans, and, as a rule, are simple. The only cervical vertebra which presents a bifid spine in all races is the axis; even this may be non-bifid in the Negro, and occasionally in the European." Frazer (4) also states: "the seventh spine is non-bifid, and this is frequently the case also in the sixth—a condition normal in the lower races."

The fact remains that we know little of the true conditions obtaining in the Nordic, Alpine or Mediterranean racial strains of the Caucasian stock, while the details of the cervical spinous processes in the Negroid, Mongoloid or Australoid peoples have not yet been investigated.

It is generally assumed that the Negroid peoples present characters which are primitive, and consequently nearer to those which were possessed by the anthropoidal stock from which Man has been derived.

It was because I had noted, while examining the collection of Negroid skeletons in Johannesburg, the recurrence of features very different from those characteristic of the European cervical vertebrae, that I decided to make a detailed analysis of the cervical spinous processes in the Bantu and Bushman peoples with a view to disclosing any primitive features of anthropological significance. It is necessary from the outset to insist on precision in terminology. The term generally used to describe the bisected condition of the cervical spinous processes in the European is "bifid." There is more than one type of bifid cervical spinous process. "Bifid" means no more than bisected or bipartite, and conveys no sense of divergence on the part of the sections. Divergence of the sections is characteristic of the European cervical spinous processes and would be more adequately expressed by "bifurcate." A second type of "bifid" cervical spinous process has been found in the Bantu, in which the sections do not diverge; this type I have named "cleft." I prefer the term "bifurcate" because occasionally confusion arises in the use of the term "bifid spine," which might very justly be expected to bear an exact equivalence with the Latin form "spina bifida." In the Negroid races the greater number of cervical spinous processes are not bifid or bisected and present a variety of different forms. It has been found necessary to describe four different forms, and to suggest names.

My classification of cervical spinous processes is as follows:

A. *Bifid.*
   (1) Bifurcate.
   (2) Cleft.

B. *Non-bifid.*
   (1) Acute.
   (2) Obtuse.
   (3) Pediculate.
   (4) Clavate.

II. MATERIAL

The skeletons contained in the Anthropological Museum of the Anatomy Department of the University of the Witwatersrand have provided the bulk of the material for this report. This material includes the vertebral columns of 71 Bantu natives, of one Bushman and of 11 Europeans. The Witwatersrand collection is enriched by certain skeletons temporarily loaned by the Curator of the McGregor Museum of Kimberley. These skeletons have formed a most valuable supplement, indeed, they have formed almost all the Bushman material used in the preparation of this report. Thus the total numbers of vertebral columns examined are as follows: Bantu, 71; Bushman, 12; European, 11.

III. THE OCCURRENCE OF BIFID CERVICAL SPINOUS PROCESSES IN EUROPEAN, BANTU AND BUSHMAN

It has been suggested in the introduction that fossil Man and the lower races of extant Man on the one hand, and European Man on the other, present features of distinction in respect of the bisected or bifid condition of the spinous processes of the cervical vertebrate. The skeletal material summarised above has been surveyed in order to determine the proportions in which the cervical spinous processes of the European, Bantu and Bushman races of Man are bifid, the results of the survey being set out in fig. 1. On the base line are set out the designations of the lower six cervical vertebrate from left to right in descending order. Rectangles have been constructed above the horizontal designation of each vertebra, each of a height proportional to the number of specimens of each vertebra which have been examined. The rectangles have been subdivided into black and white areas, which represent the numbers of vertebrae of each denomination of which the spinous processes are respectively bifid and non-bifid. Separate graphs for the European, Bantu and Bushman have been constructed. Inequalities in height of the rectangles within each of the three graphs is due to loss or damage to the spinous processes of a few vertebrae.

In every specimen the condition of the spinous process, whether bifid or not, has been determined by its appearance in norma verticalis. The sharp but shallow dorsal groove, which occasionally marks the spinous processes of the vertebrae of any region, has been disregarded in making this computation. Such shallow grooves seldom exceed a millimetre in depth, and, while held to be reminiscent of a bipartite stage in the development of a spinous process, are not considered to be of deeper significance. Account has been taken only of those spinous processes in which the dorsal division is deep, or decisive in its effect on the contour of the whole spinous process.

Table I shows the proportions of bifid and non-bifid spinous processes found in the European, Bantu and Bushman cervical columns, and contains the data upon which the graphs in fig. 1 are constructed.

The numbers of European and Bushman vertebrae are both small, but, if it be permitted to render small numbers in percentages, the resulting values afford ground for an important inference concerning the relationship of the

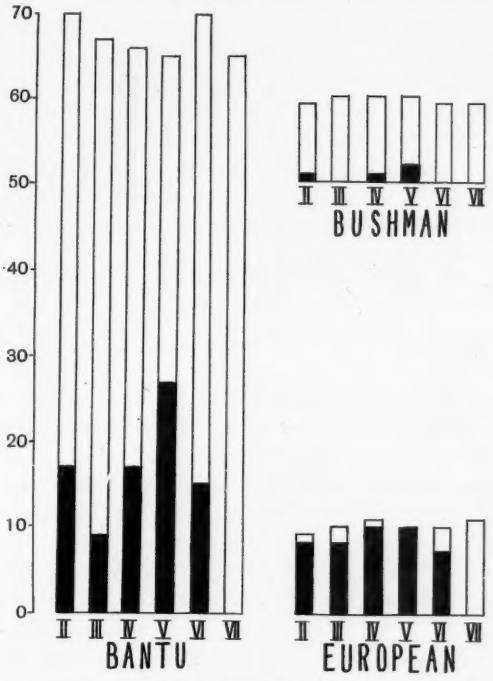

Fig. 1. This figure presents in graphic form the distribution of bifid cervical spinous processes in the European, Bantu and Bushman races of Man. On the base lines from left to right are the designations of the cervical vertebrae, with the exception of the atlas, in descending order. Rectangles in white represent non-bifid cervical spinous processes and those in black bifid. Actual numbers are indicated by the scale on the left.

Table I. *Bifid and non-bifid cervical spinous processes in European, Bantu and Bushman*

		Vertebra							
		II	III	IV	V	VI	VII	Totals	%
European	Bifid	8	8	10	10	7	0	43	71·6
	Non-bifid	1	2	1	0	3	10	17	28·3
Bantu	Bifid	17	9	17	27	15	0	85	21·2
	Non-bifid	53	58	48	38	55	65	317	78·8
Bushman	Bifid	2	0	1	2	0	0	5	7·1
	Non-bifid	9	12	10	10	12	12	65	92·8

three races. If we accept the proportions of bifid cervical spinous processes as inferential approximations of 71·6 per cent. for the European and of 7·1 per

cent. for the Bushman, a striking contrast appears. The observed proportion of bifid cervical spinous processes for the Bantu, viz. 21·2 per cent., lies between the other two, but much nearer to the Bushman than to the European. The proportions of bifid cervical spinous processes, therefore, afford statistical evidence which is in harmony with the accepted facts of habitat, colour and hair form, notwithstanding difference of stature, of a closer relationship between Bantu and Bushman than between either of these and the European.

It seems that of the middle three vertebrae the fifth most constantly presents a bifid condition of the spinous process in all three races. In this my observations agree with those of Von Eggeling(5) but disagree with those of Cunningham(6), who regards the third or fourth as most constant. Both of these authors worked on a mixed series of the skeletons of the coloured races.

IV. DIFFERENT TYPES OF BIFID CERVICAL SPINOUS PROCESSES

The attention of the reader is directed to fig. 2, which presents tracings of four different cervical columns.

In preparing this figure, the vertebrae were carefully orientated in norma verticalis and tracings were made of natural size with a dioptograph. A centimetre scale at the side shows scale of reduction.

The spinous processes of the column on the right (No. 240) exhibit a bifid condition in the fourth and fifth members. In the other three columns the condition of the majority of the spinous processes of the vertebrae from the third to the sixth inclusive is also bifid, but a contrast is provided. Although many of the spinous processes in the two middle columns (Nos. 152 and A 78) are not deeply cut by the dorsal groove, yet, regarding the whole of their contours, it is evident that they are subdivided into two lateral divergent alae. The spinous processes of the fourth and fifth vertebrae of No. 240, on the right, are cut by deep narrow grooves into two dorsal sections which maintain their parallelism. It is proposed to name these two varieties of bifid cervical spinous processes as follows:

(1) *Bifurcate*, the type in which two sections diverge, of which examples are seen in the middle members of columns Nos. 152, A 78 and 115.

(2) *Cleft*, the type in which the two sections do not diverge and of which the fourth and fifth members of No. 240 furnish examples.

These distinctions are of importance, because it is the bifurcate type which is characteristic of the cervical column of the European.

Using these designations, bifurcate and cleft, Table II is drawn up to show the proportions in which these two types of bifid spinous processes occurred in the European, Bantu and Bushman cervical columns.

Table II shows that the cervical spinous processes most characteristic of Europeans are not merely bifid, but bifurcate. The bifurcate spinous processes are in numerical excess of cleft in each of the three races, but the proportion of cleft to bifurcate is highest in the Bantu and lowest in the European. It

may well be that the cleft type represents a retrogressive form. This speculation receives some support from the fact that a number of cleft spinous processes greater than two was not found among the third, fourth, fifth and sixth

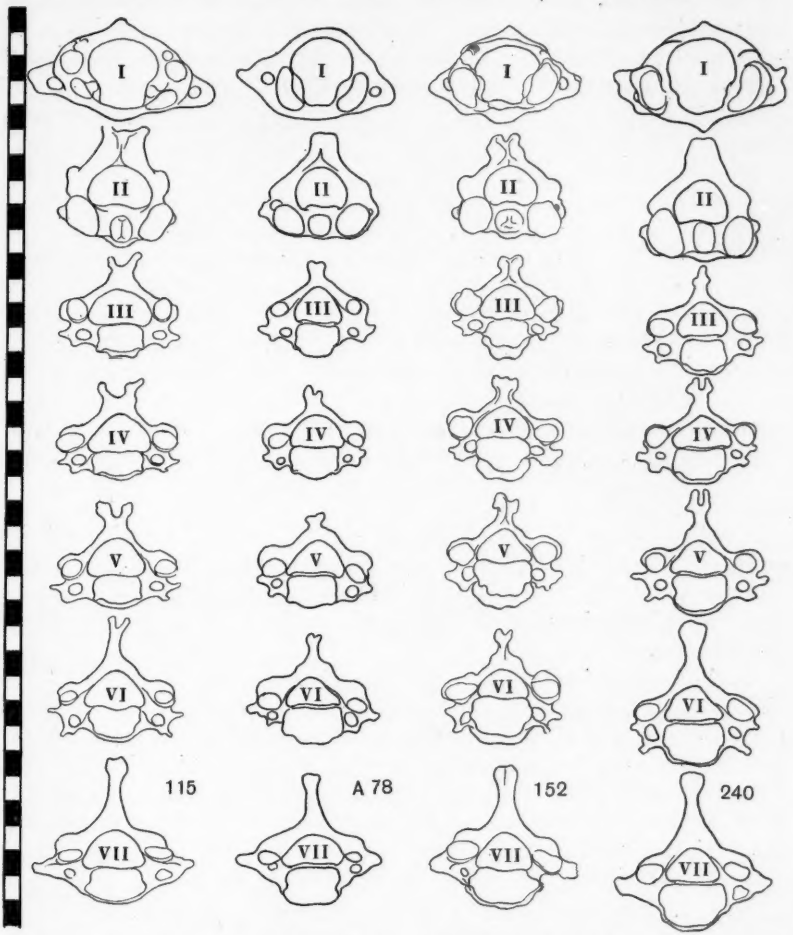

Fig. 2. Four tracings of cervical columns in norma verticalis are shown in this figure. Column No. 115 on the left is European, of Nordic type, No. A 78 is also European, but Mediterranean, while No. 152 is Bantu. These three tracings illustrate bifurcate spinous processes. The column on the right, No. 240, illustrates the cleft type in its fourth and fifth members. A centimetre scale is shown on the left of the tracings.

members of any one column. The cleft type occurs then, not as a uniform series, but associated with some other type of spinous process. Indeed, the cleft type has been seen in association with every other type described in this

paper, bifid or non-bifid, and with more than one other type in the same cervical column.

In only 4 out of 61 intact Bantu columns were the spinous processes of the four vertebrae, third to sixth, all bifid. In 2 of these the type of all the four was bifurcate, and in 2 the bifurcate and cleft types were mingled. Cleft types were found in 18 columns and bifurcate in 19, but the combination of cleft and bifurcate was found in 6 columns only.

Table II. *Bifurcate and cleft cervical spinous processes in the European, Bantu and Bushman*

		Vertebra							
		II	III	IV	V	VI	VII	Totals	%
European	Bifurcate	5	7	8	8	3	0	31	51·6
	Cleft	3	1	2	2	4	0	12	20·0
	Other forms	1	2	1	0	3	10	17	26·3
	Totals	9	10	11	10	10	10	60	
Bantu	Bifurcate	9	6	11	13	9	0	48	11·94
	Cleft	8	3	6	14	6	0	37	9·20
	Other forms	53	58	48	38	55	65	317	78·85
	Totals	70	67	65	65	70	65	402	
Bushman	Bifurcate	1	0	1	1	0	0	3	4·28
	Cleft	1	0	0	1	0	0	2	2·85
	Other forms	9	12	10	10	12	12	65	92·80
	Totals	11	12	11	12	12	12	70	

Combinations of the cleft type with various types of non-bifid spinous processes (*vide* Section VI) occurred as follows: with pediculate in 15, with acute in 3, and with obtuse in 2 cervical columns. These figures will give the reader some indication of the heteromorphism of the cervical spinous processes in the Bantu.

A close connection is shown, on the one hand, between the cleft and the bifurcate types, and, on the other hand, between the cleft and the non-bifid pediculate types. Probably the cleft type is retrogressive, and perhaps in the evolutionary sense lies intermediate between bifurcate and pediculate types. It has not proved possible to draw any inferences as to the tribe of a Bantu skeleton from the presence of either bifurcate or cleft spinous processes in the cervical column.

V. BIFURCATE CERVICAL SPINOUS PROCESSES IN THE EUROPEAN AND IN THE BANTU

It has been stated in Section IV that Bantu columns containing 4 bifid spinous processes below the axis are uncommon (4 out of 61). Only 2 Bantu cervical columns contained spinous processes of uniform bifurcate type, and one of these, No. 152, is shown in fig. 2. This column should be compared with that on the extreme left, No. 115, which is European. To one who has been accustomed to handling skeletons in a London Anatomy school, the series on the left, No. 115, makes appeal as typical of the European. A reference

to the figures in any British text-book on Anatomy will confirm this impression, which is gained from consideration of the robust nature of the spinous processes, the length of the sections and the wide angle of their divergence. The intermediate series, A 78, presents a contrast in certain respects. The average spinous process is less robust, less conspicuously bisected; the lateral alae are shorter and the angle of their divergence is smaller. Skeleton A 78 is also European, but is one of a series derived from a Sardinian sepulture and presented to the University of the Witwatersrand by Prof. Frasetto of Bologna. The European material for this paper is made up of 11 skeletons of which 6 are Sardinian. Of the other 5, 3 are mounted skeletons supplied from London, and 2, which include No. 115, were prepared locally. A 78 will serve as an example of the Sardinian, and No. 115 as an example of the Northern European cervical column. The characters indicated above are constant in the two series. A sufficiency of material to investigate the point fully is not available, but it is suggested that the cervical spinous process of robust type, with long and widely divergent alae, the unequivocal "bifurcate" type, is characteristic of the Northern European and that the less robust type, with shorter alae and less unequivocally bifurcate, is representative of the Mediterranean peoples. The point relevant to a report on the cervical spinous processes of the South African native races is that bifurcate cervical spinous processes in the Bantu are usually of the "Mediterranean" type.

Using the descriptions given above to indicate types of bifurcation, which may be called "Nordic" and "Mediterranean," it was found possible, out of the 48 bifurcate spinous processes of Bantu cervical columns (*vide* Table II) to refer 10 to the Nordic and 38 to the Mediterranean type. This finding raises the question: does the Mediterranean type of bifurcation represent an early stage of a retrograde change, antecedent, perhaps, to that state which I have called "cleft"? Or does the Mediterranean type stand for actual admixture between Arabs or other Mediterranean peoples and Bantus, perhaps on the East Coast of Africa? In view of the tendency in Man to reproduce primitive forms in the cervical spinous processes, which is demonstrated later in the Bantu and in the Bushman, I prefer the first of the two alternatives outlined above.

VI. THE NON-BIFID CERVICAL SPINOUS PROCESSES

Attention has already been drawn to the multiplicity of form exhibited by the cervical spinous processes, during the survey of the bifid types in Section IV. In order to illustrate the variety of forms met with among non-bifid cervical spinous processes, there are represented in fig. 3 three Bantu and one Bushman cervical columns. From the appearances presented in norma verticalis there may be recognised four different types of non-bifid spinous processes to which the names acute, obtuse, pediculate, and clavate have been given. Descriptions of these four types will follow *seriatim*.

Acute. This name applies to those flat-sided spinous processes that terminate

by tapering to a point. They are slender and are usually long compared with other types, being often over a centimetre in length. In fig. 3 this type is illustrated in the Bantu column, No. 263, and in the Bushman column, MMK 144, on the extreme right.

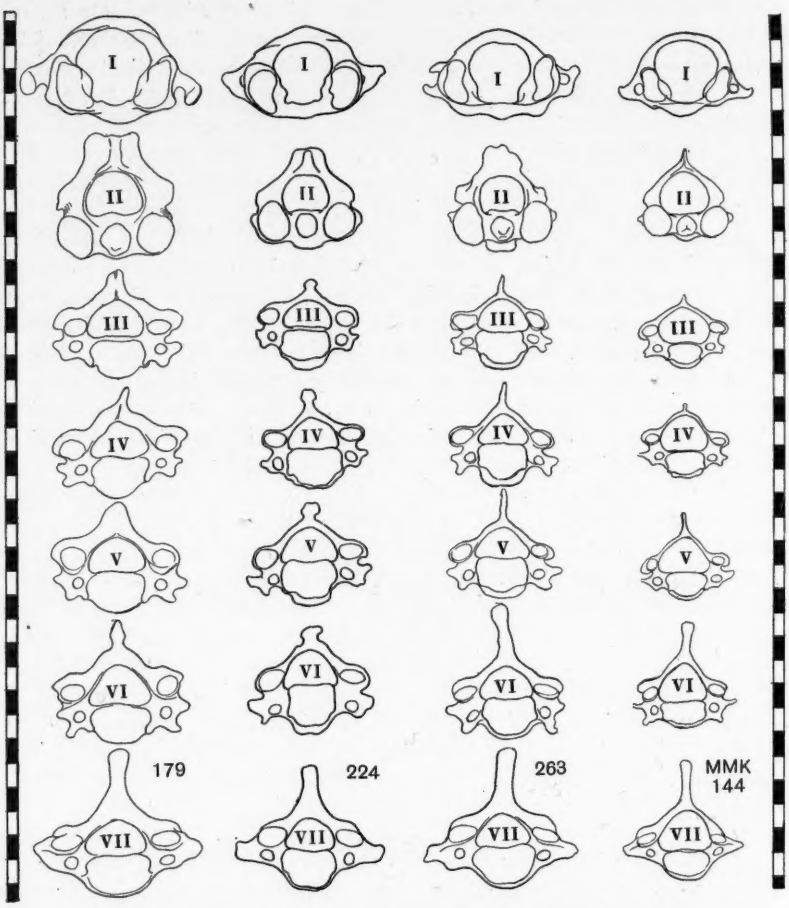

Fig. 3. This figure illustrates the four types of non-bifid cervical spinous processes. Vertebrae III, IV and V of No. 179 on the left show the obtuse type. The pediculate type is shown in vertebrae III to VI of No. 224. The columns Nos. 263 and MMK 144 illustrate the acute type. The clavate type is shown in each seventh vertebra.

MMK 144 is a Bushman and the others are Bantu, the difference of size and build is evident. The scale at the side is in centimetres.

Obtuse. This name is intended to suggest a contrast with the last. Spinous processes of this type are blunt-ended, irregular bony prominences showing

no differentiation for attachment of muscle or ligament. They are often pyramidal or conical in shape, but seldom attain the length of a centimetre. Examples are shown in the third, fourth and fifth members of the Bantu column No. 179 in fig. 3.

Pediculate. These spinous processes are stud-like and are distinguished from both the foregoing by a short pedicle, which separates a blunt expanded dorsal end from the point of attachment. The length of a specimen of this type may be a centimetre, but is certainly less than that of the type next to be described. There are four examples in fig. 3 in the Bantu column No. 224, and one in the sixth member of No. 179.

Clavate. This type of spinous process is long and club-shaped, having an elongated neck which tapers to the middle, both from the point of attachment and from the dorsal termination. This description applies, in the main, to the prominent spinous process of the seventh cervical vertebra. It follows that specimens of the clavate type in length greatly exceed the other types.

Table III. *The non-bifid cervical spinous processes*

		Vertebrae					
		III	IV	V	VI	VII	Totals
Bantu	Acute	6	8	7	0	0	21
	Obtuse	11	10	5	0	0	26
	Pediculate	41	30	24	19	1	115
	Clavate	0	0	2	36	64	102
	Totals	58	48	38	55	65	264
Bushman	Acute	5	2	2	1	0	10
	Obtuse	2	3	1	0	0	6
	Pediculate	5	5	5	1	1	17
	Clavate	0	0	2	10	11	23
	Totals	12	10	10	12	12	56

Table III shows the observed frequency of occurrence of each type of non-bifid spinous processes in the lower five cervical vertebrae of my Bantu and Bushman columns.

In the Bantu the predominant type is evidently pediculate, but in the Bushman the acute type is rather more numerous and the pediculate type is corrrespondingly reduced. In the Bantu, the 21 spinous processes of acute type were contained in 9 different columns, the 115 of pediculate type in 44 columns and the 26 of obtuse type in 13 columns. When it is stated that a set of the middle three cervical vertebrae possessing spinous processes of one type only was found in no more than 20 out of 71 columns, the essential heteromorphism of the cervical spinous processes in the Bantu will be appreciated.

The types of spinous process contained in these 20 columns were distributed as follows: acute 3 out of 9, pediculate 13 out of 44, and obtuse 4 out of 13 columns which contained those types in some association or another. No Bantu tribe can be associated with any one type of cervical spinous process. The 3 columns containing spinous processes of uniform acute type were divided

between two Zulus and a Bantu of unknown tribe, the 13 pediculate columns were divided among nine different tribes and the 4 obtuse columns among four tribes. An attempt has been made to determine if there be a predominant type of cervical spinous process in the Bushman. The small slender bones of the Bushman are very distinctive. A little familiarity in handling these skeletons will enable an observer to recognise the Bushman type with precision. By a reference to the series on the right in fig. 3 (MMK 144), or the middle series in fig. 5 (MMK 163) the reader will appreciate the essential difference of size and build between Bushman and Bantu skeletons. After selecting Bushman skeletons which seemed most typical in point of size, a second test, that of skull form, was applied in order to obtain Bushman material of the purest. It has been shown by the recent work of J. H. Gear (7) that the predominant skull form of the Bushman is that known in the terminology of Frasetto (8) as chamae-pentagonoid. From the same material as that on which Gear worked and by the courtesy of that worker, who placed his results at my disposal, I have been able to select cervical columns from Bushman skeletons which satisfy, not only the criterion of size, but that of skull form also.

Four such cervical columns were selected (MMK 144, 165, 174, 186) and the spinous processes were examined. It was found impossible to identify any type of cervical spinous process as predominant or characteristic. One column contained 3 pediculate spinous processes (MMK 186), a second 3 acute (MMK 144), a third 2 obtuse with the fifth, sixth and seventh all clavate (MMK 174), and the fourth contained a specimen of the three types. The conclusion is that no one characteristic Bushman type of cervical spinous process is revealed by the material available.

VII. THE SPINOUS PROCESS OF THE AXIS VERTEBRA

Morris' *Treatise on Anatomy* alone, out of six text-books consulted, recognises the occurrence of a non-bifid spine to the axis vertebra. "The only cervical vertebra which presents a bifid spine in all races is the axis; even this may be non-bifid in the Negro and occasionally in the European" (3). Other authorities represent the axis' spinous process as invariably bifid and with the two alae widely divergent. It will be shown that in the Bantu and in the Bushman races the spinous process of the axis presents a great variety of form.

The drawings of the Bantu axis in fig. 4 have been made by surveying the axis both in norma verticalis and in norma dorsalis. Tracings of natural size have been made in both normae and are reproduced, in every case, with the norma verticalis immediately above the norma dorsalis, and accompanied by a centimetre scale. In the axis of common description (European), the spinous process has divergent alae when viewed in norma verticalis; in norma dorsalis, the spinous process presents the appearance of an inverted "Y,"

like 1 in fig. 4. Aberrant forms arise when the median ridge which forms the stem of the inverted "Y" is shortened to such an extent as to form a "V," also inverted, a condition shown in fig. 4, 3; or, if divergence of the alae is excessive, a "T" is substituted for "Y," as in fig. 4, 5; or again, if divergence is slight and the median ridge is abbreviated, a "U" form may replace "Y" or "T." Further, in norma verticalis the spinous process may be bifurcate

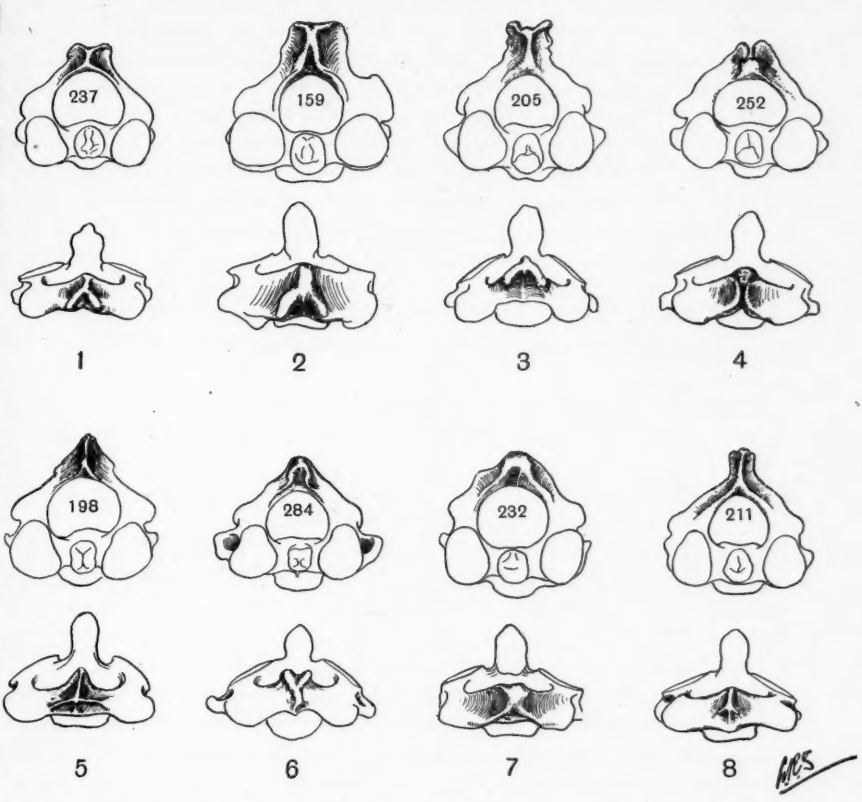

Fig. 4. In this figure are shown tracings of different forms of the spinous process of the axis. A centimetre scale is set at the left side. In each example a tracing in norma verticalis lies above the tracing in norma dorsalis of the same vertebra.

with divergent alae, as in fig 4, 1 and 3, or divergence may be absent and a cleft form result, as in fig. 4, 4.

In the Bantu the bifid character may be entirely lacking and a spinous process which is obtuse in norma verticalis may result, as is shown by 5, 6, and 7 in fig. 4. In norma dorsalis 5 shows a "T" form, but 7 shows a rounded tubercle in both normae. A common Bantu form is that represented in fig. 4, 2,

in which the spinous process is flat-topped in norma verticalis and presents a "Y" form in norma dorsalis.

Table IV shows the proportional incidence of the various forms of the spinous process of the axis, considered in two normae, and the different combinations of form in the two normae.

The spinous process of the Bantu axis, therefore, exhibits division of some degree in a majority of cases. Examination in norma verticalis reveals a bifid condition in 17 out of 70 (the sum of bifurcate and cleft forms), and in norma dorsalis in 52 out of 70 (the sum of Y, V and U forms). These figures may be compared with 7 out of 9 bifid in norma verticalis, and 8 out of 9 in norma dorsalis, for the European axis. In the Bushman only 1 out of 9 was bifid when viewed in norma verticalis, but in norma dorsalis 6 out of 9 show some trace of division; proportions which are not very different from those found in the Bantu.

Table IV

		Norma dorsalis					
		Inverted					
	Norma verticalis	Y	V	U	T	Other forms	Totals
Bantu	Bifurcate	8	1	0	0	0	9
	Cleft	4	2	1	0	1	8
	Flat	14	5	0	4	0	23
	Obtuse	13	4	0	9	4	30
	Totals	39	12	1	13	5	70
Bushman	Bifurcate	1	0	0	0	0	1
	Cleft	0	0	0	0	0	0
	Flat	2	0	0	0	0	2
	Obtuse	0	2	1	0	1	4
	Other forms	0	0	0	0	2	2
	Totals	3	2	1	0	3	9
European	Bifurcate	5	0	0	0	0	5
	Cleft	2	0	0	1	0	3
	Flat	1	0	0	0	0	1
	Totals	8	0	0	1	0	9

Summary. Specimens of the axis in which the spinous process is divided in one norma or the other are, in the Bantu 52 out of 70, in the Bushman 6 out of 9, and in the European 9 out of 9. It is interesting to note that variants of the bifurcate, inverted "Y" type of spinous process occur in the European even in a short series. These variations, it will be noted, have their counterparts in both Bantu and Bushman.

Anomalous forms of the axis' spinous process

Table IV shows that certain forms occur which do not lend themselves to classification in terms of varying degrees of bisection or of divergence of sections. Five out of 70 Bantu, and 3 out of 9 Bushman specimens of the axis

presented anomalous forms in the spinous processes. A higher proportion of variability, therefore, appears in the Bushman than in the Bantu axis.

It may be of interest to consider briefly the characters of these anomalous or bizarre forms.

(1) Bantu Nos. 232 and 292. No. 232 is shown in fig. 4, 7. There is no trace of bisection, the spinous process is obtuse in both normae. A Bushman axis (MMK 163) presents a similar appearance, and Le Double (9) records a similar form in a European axis.

(2) Bantu No. 211, fig. 4, 8. The spinous process gives an obtuse appearance in norma verticalis, without trace of bisection; in norma dorsalis two ridges cross the summit at right angles and give a cruciate ridged appearance. A similar specimen was found in a Bushman skeleton (MMK 163), and in the axis of a gorilla.

(3) Bantu No. 284, fig. 4, 6. The common appearance of an inverted "Y" seen in norma dorsalis is reversed. The "Y" appears with the stem directed tailward and with the divergent alae headward. In norma verticalis this spinous process is obtuse.

(4) Bantu No. 252, fig. 4, 4. The spinous process is cleft in both normae, but a rounded tubercle replaces the stem of the inverted "Y," and is separate from the alae.

(5) Bushman, MMK 144. The spinous process is acute in norma verticalis, and presents a thin vertical ridge in norma dorsalis. A tracing is shown in fig. 3.

VIII. THE ANGLE OF INCLINATION OF THE CERVICAL SPINOUS PROCESSES

The lateral views of 5 cervical columns are shown in fig. 5. The column on the left is that of a chimpanzee. Second from the left is a reproduction of the drawing of the cervical vertebrae of La Chapelle Man which appears in fig. 139 of Boule's *Fossil Man* (10). I wish to make all acknowledgement of my indebtedness to Prof. Boule. In the original the figure is one-half natural size: my tracing was made double the size of fig. 139, in order that the result may be compared with my other tracings, which were of natural size. Reduction has now affected all 5 columns in the same proportion.

From the left in succession after La Chapelle Man, the tracings are those of the cervical columns of a Bushman, a Bantu and a European. Care was taken to ensure that each of these three columns was intact, otherwise they were taken at random and unselected. Except for La Chapelle Man, the columns represented in fig. 5 were set in plasticene in a true lateral position, with a nice approximation of the intervertebral articular facets, and dioptograph tracings of natural size were made. The angles are deduced from the dioptograph tracings by the following method. Straight lines were drawn as follows: (1) through the centre of the root and the most prominent point of each spinous process; (2) along the plane of the front of each vertebral body.

The inferior angle subtended between these two lines is taken as the angle

of inclination of the spinous process with the vertebral body. These angles are set out on the right of each spinous process in fig. 5. It is unfortunate that only the lower three cervical vertebrae of La Chapelle Man have been preserved, but the angles of inclination of their spinous processes have been deduced from the tracing of Boule's figure by the same method.

Regarding the whole series of cervical columns, no very striking difference appears between the angles of inclination of the spinous processes of the three columns on the right, but there is a contrast between any of these three and either La Chapelle Man or the chimpanzee in this same respect. A closer analysis of the average angle of inclination of the two lowest cervical spinous processes shows that there is a wide separation between any of these three races of living Man and La Chapelle Man in the inclination of the sixth and seventh spinous processes.

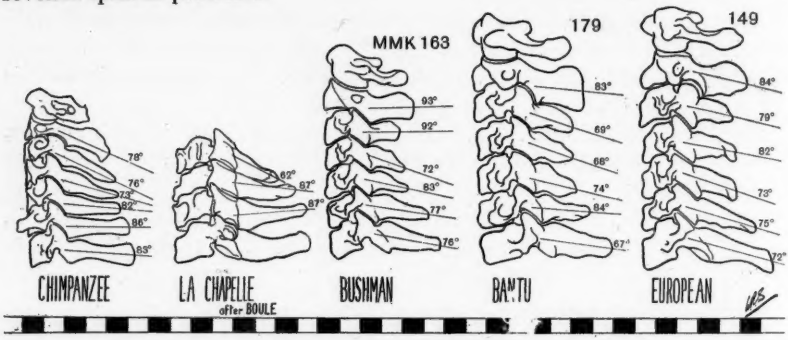

Fig. 5. This figure presents tracings of five cervical columns in norma lateralis in order to show the angles of inclination of the spinous processes. All the tracings were made from skeletons in the Anatomy Department with the exception of the second from the left, which has been adapted from fig. 139 of Boule's *Fossil Man*. The angles between the spinous processes and the front of the vertebral bodies are marked opposite the spinous processes.
A centimetre scale accompanies the tracings.

Averages of the angles of inclination of the sixth and seventh cervical spinous processes are as follows: European 73½°, Bantu 75½° and Bushman 76½°, but the corresponding values for La Chapelle Man and for the chimpanzee are 87° and 84½°. La Chapelle Man is therefore much nearer to the anthropoid in this respect than to living Man; and the Bushman approaches slightly nearer to fossil Man and to the anthropoid than do either the Bantu or the European. In addition, the shortening of the cervical spinous processes in the Bantu may be noted.

In Table VI are set out the angles of inclination of the cervical spinous processes deduced from the tracings in fig. 5.

It may be stated, then, that though the Negroid races of Man present many primitive features in the forms of their cervical spinous processes, in the angles of inclination of their lowest members primitive features have been lost.

A primitive feature, however, is revealed the angle of inclination of the second and third cervical spinous processes of e Bushman column, MMK 163. The tracing shows that these spinous processes differ from the second and third members of the other human columns shown in fig. 5, in that they are sloped slightly cephalad of the horizontal plane. In the Bushman column the inferior angle of inclination measures 93° for the second and 92° for the third cervical spinous processes. The values of this angle in the Bantu (No. 179) and in the European (No. 149) are 83° and 84° for the second, and 69° and 79° for the third. A similar headward slope of the second and third cervical spinous processes, and of these only, was found in the skeletons of a gorilla and of a gibbon, but not in the chimpanzee skeleton which was used for the tracing in fig. 5. This primitive inclination of the second and third spinous processes is not uncommon in the Bushman.

Table V. *Degrees of inclination of spinous processes*

	Reference	Vertebrae II	III	IV	V	VI	VII	Average of VI and VII
European	149	84	79	82	73	75	72	73½°
Bantu	179	83	69	68	74	84	67	75½°
Bushman	MMK 163	93	92	72	83	77	76	76½°
La Chapelle	Boule	—	—	—	62	87	87	87°
Chimpanzee	—	78	76	73	82	86	83	84½°

IX. COMPARATIVE ANATOMY

The comparative series of skeletons in the Anatomy Department is somewhat limited, but is probably fairly representative, as it includes the skeletons of 7 anthropoids, 3 lem and other mammalian forms.

The terminology devised to describe the forms of the cervical spinous processes in Man was found to be readily applicable to those of the lower forms.

In Table VI are set out the descriptions of the types of cervical spinous processes found in different animal forms in the course of this survey.

It was found that all the forms of cervical spinous process found in the comparative series and detailed in Table VI have their counterparts in Man. The converse, however, is not the case; not all the types described in Man were identified in the comparative series, for the cleft type, except in the axis, was not found. So far as it goes, this negative finding supports the view, already expressed, that the cleft type is retrogressive. The comparative material available has not revealed this type as primitive.

The spinous process of the axis

The axis, being so much a distinct anatomical and physiological entity, has been treated separately in the earlier pages, and will receive separate treatment in this section.

The spinous process of the axis presents features which may be interpreted as primitive, almost as frequently as do the spinous processes of the

lower cervical vertebrae. The strongly marked bifurcate quality is frequently lost in the spinous process of the Negroid axis. Examples of the axis in which the spinous process is cleft rather than bifurcate or in which it lacks cleavage and presents an anomalous form, occur frequently in the Bantu and still more frequently in the Bushman. It may be noted that such forms are not rare in the European. A bifurcate spinous process was not found among the Primates examined, though a cleft form was found in *Macacus Rhesus*. The types of axis' spinous process called flat or obtuse in norma verticalis and associated with inverted Y, T or V forms in norma dorsalis were found in Primates (*vide* Table VI). Many of the other anomalous forms described in Section VII also have their counterparts in Primates. The obtuse form with cruciate dorsal ridges (fig. 4, 6) resembles a form found in a gorilla axis. The form with an acute spinous process, noted in the Bushman (Section VI and fig. 3) is common among monkeys. The obtuse and tuberculate form found twice in the Bantu series (Section VII and fig. 4, 7) was found in a chimpanzee.

Table VI. *The types of cervical spinous processes in the anthropoids, monkeys and other forms*

	Vertebra						
	II		III	IV	V	VI	VII
	Norma verticalis	Norma dorsalis					
Gorilla	Obtuse	Cruciate	Clav.	Clav.	Clav.	Clav.	Clav.
Chimpanzee (1)	Flat	V	Clav.	Clav.	Clav.	Clav.	Clav.
„ (2)	Obtuse	Tubercle	Ac.	Ac.	Ac.	Clav.	Clav.
„ (3)	Obtuse	Tubercle	Ac.	Ac.	Clav.	Clav.	Clav.
„ (4)	Obtuse	V	Obt.	Obt.	Ac.	Clav.	Clav.
Orang	Clavate	Ridge	Clav.	Clav.	Clav.	Clav.	Clav.
Gibbon	Pediculate	Y	Ped.	Ped.	Ped.	Ped.	Ped.
Hapale Jacchus (1) ...	Acute	Ridge	Ac.	Ac.	Ac.	Ac.	Ac.
„ „ (2) ...	Flat	Y	Ac.	Ac.	Ac.	Ac.	Ac.
Macacus Rhesus	Cleft	Y	Ped.	Ped.	Ac.	Ac.	Ac.
Cebus Fatuellus	Acute	Ridge	Ac.	Ac.	Ac.	Ac.	Clav.
Mycetes Seniculus ...	Acute	Ridge	Bif.	Bif.	Ac.	Ac.	Clav.
Cynocephalus Hamadryas	Acute	Ridge	Ac.	Ac.	Ac.	Ac.	Ac.
Lemur Catta	Acute	Ridge	Ped.	Ped.	Ped.	Ped.	Ped.
„ *melanocephalus* ...	Acute	Ridge	Ac.	Ac.	Ac.	Ac.	Ac.
„ *variagatus* ...	Acute	Ridge	Ped.	Ped.	Ped.	Ped.	Ped.
Didelphys cancrivora ...	Obtuse	Tubercle	Obt.	Obt.	Obt.	Obt.	Obt.

The lower cervical spinous processes

In the gorilla and the orang the predominant type is the clavate. This type is less conspicuous in the chimpanzee and is found only occasionally in monkeys and then has a tendency to appear at the lower end of the cervical column. Evidently the clavate type is anthropoid, for it is found throughout the cervical column in the gorilla and the orang.

In the gibbon a whole series of pediculate cervical spinous processes was found. Perhaps this represents the retention of a primitive condition on the part of the gibbon, because with very few exceptions the type was found in lemurs but not elsewhere among Primates. Two genera of lemurs were found

to have a complete series of pediculate cervical spinous processes. The acute type is found occasionally among anthropoids, but most commonly in monkeys. The obtuse type seems to be sub-Primate in position. A complete series was found in the opossum, *Didelphys cancrivora*, but in Primates, except in the axis, the type is of rare occurrence. It may be stated, therefore, that anthropoid types are reproduced in both the clavate and the pediculate cervical spinous processes; a sub-anthropoid primate type is reproduced in the acute, and a sub-Primate type in the obtuse cervical spinous processes. The Negroid races of South Africa may be considered to present primitive features in a high degree. Table II in Section IV shows that the non-bifid cervical spinous processes, of which every type has been identified in this comparative series, account for 78 per cent. of the total in the Bantu and for 92 per cent. in the Bushman.

The bifurcate type

The position of the bifurcate type is of some interest. Bisection of the spinous processes has been observed in fossil reptiles, so the capacity of even sub-mammalian vertebrates to evolve a bifid type is clear. R. S. Lull (11) remarks "the neural spines, which are usually single, are here (in *Diplodocus*) deeply cleft from the third cervical to the sixth dorsal, indicating the pairing of the great muscles which run along the mid-dorsal line of the back, and the independent action of the two members of the pair. This, of course, is indicative of a wide lateral sweeping of the head and neck." The same author uses the character of bisection as a means of classification of Sauropoda. Bifurcate cervical spinous processes were found in the monkey *Mycetes Seniculus*, so the capacity of Primates to evolve cervical spinous processes, which are not only bifid but bifurcate, is clear irrespective of the assumption of the erect attitude.

X. General discussion

The fact that bifurcate spinous processes are to a very high degree characteristic of the European cervical column emerges very clearly from the foregoing pages. What circumstances have favoured the evolution of cervical spinous processes of this type in Europeans, and their replacement by primitive types in the Negroid races, is a matter for speculation. It might be surmised that the explanation lies in some circumstances related to posture and habitus.

Cunningham (12) pronounces a clear opinion when he writes "non-bifid spines in the lower races...indicate a freer mobility of the vertebral column, coincident with other arrangements of the lower races which lend the lumbar region a greater mobility."

Von Eggeling (13) from extended comparative studies of the skeleton and of the muscular systems of man, anthropoids and monkeys makes the deduction that variations in the bifurcation of the cervical spinous processes depends on posture and on the mobility of the cervical spine. The non-bifid condition of the cervical spinous processes of the apes and the monkeys, in Von Eggeling's

opinion, is associated with the non-attainment or the incomplete attainment of the movement of erection of the cervical spine. This author attributes a great influence in particular to the degree of development of the muscle semispinalis cervicis. The difference in the opinions expressed by these two authors is interesting: while Cunningham connects the non-bifid condition with greater mobility, Von Eggeling finds lesser mobility the more obvious association.

Von Eggeling also contributes some very interesting observations on the development of the cervical spinous processes. It seems that in European foetuses the "bifid" condition of the spinous processes can be recognised during the cartilaginous stage of development. Even the commonly non-bifid sixth and the seventh spinous processes exhibit the bifid condition in the cartilaginous stage, not constantly indeed, but in a far higher proportion than in the mature skeleton.

In the second half of the first year bifurcation of the cervical spinous processes begins to disappear, first at the seventh and thence in a cranial direction. Up to puberty bifurcation of the sixth spinous process becomes less frequent with increasing age.

A just interpretation of these observations is not easy; perhaps the most obvious is that the bifid quality of the cervical spinous processes in Europeans is a recession. This suggestion, prompted by ontogeny, is supported by the findings recorded in Section III. Non-bifid spinous processes occur in the five lower members of the European cervical column in proportions which, though much smaller than are found in the Bantu or in the Bushman column, still are not negligible.

It would seem that the change of type of the cervical spinous processes indicated in ontogeny, i.e. bifid to non-bifid, in the European has now attained virtual completeness in the seventh vertebra, usual occurrence in the sixth vertebra, and an appreciable frequency of incidence in the middle members of the cervical column.

To turn to the Negroid races: it has been shown that the non-bifid types of cervical spinous processes are represented by a large majority compared with the bifid types. The question arises: do the findings recorded above represent the result of a similar change, bifid to non-bifid, which has been achieved by the Negroid races with a high degree of completeness as compared with the European? Or, on the other hand, has the evolution of the Negroid races followed a path different from that traversed by the European; and have the progenitors of the Negroid races never possessed bifid cervical spinous processes?

A third alternative, namely that Negroid Man may be in a phase of acquiring the bifid character in his cervical spinous processes, may be dismissed in a few words. Every indication is contrary to the hypothesis of a progressive change. The presence, in the majority of spinous processes, of forms which reproduce those of anthropoid, sub-anthropoid and sub-primate mammals, can only indicate retrogression.

Our information as to the condition of the cervical spinous processes in primitive Man is scanty. Boule (1) has pointed out that these structures in La Chapelle Man are anthropoidal in their length and in their angles of inclination, and also that they are non-bifurcated. It may be added that it seems from Boule's figure that they are of clavate type.

In a recent paper Laing and Gear (14) report on the fossil or semi-fossil remains found at Zitzikama in South Africa. These observers describe cervical spinous processes similar to those of the La Chapelle skeleton, and presenting an affinity to the anthropoid and a contrast with modern Man in the same respects of length, inclination and non-bifurcation. In addition, Wells (15) has reported non-bifid cervical spinous processes in the fossil skeletons from the Zuurberg, near Port Elizabeth, which also present anthropoidal features of length and inclination. So far as the cervical column is concerned no point of distinction between the fossil Man of Africa or of Europe has yet been revealed. Extant European and Negroid Man alike show reduction in the length of the cervical spinous processes and reduction in the angles of their inclination when compared with primitive Man, who in these respects resembled the anthropoid.

It seems most probable that bifid cervical spinous processes were evolved from a non-bifid type. In European Man it is possible that the acquisition of the bifid quality was coeval with the reduction of length and of the angle of inclination, in a post-Neanderthal epoch.

The evidence of ontogeny, adduced by Von Eggeling, seems clear in its meaning, that the bifid quality of the cervical spinous processes in Europeans has entered on a phase of regression. The inference is that the bifid character of these processes is an impermanent or transient product of evolution, initiated in a post-Neanderthal epoch and destined to obsolescence. It remains to discuss the probable explanation of the predominant non-bifid cervical spinous processes of the Negroid races. The question is, whether or not the cervical spinous processes of the Negroid races, evolved from a non-bifid anthropoidal form, have passed through a bifid state.

Table I in Section III shows that the bifid type, which in Bantus accounts for some 20 per cent. of the total, is fairly evenly distributed through the spinous processes of the cervical column. It is difficult to explain the presence of any spinous processes of bifid type at all if the type be not archaic. It is probable, therefore, that in the course of evolution the spinous processes of the cervical vertebrae of the progenitors of the Negroid peoples have passed through these changes: first, the anthropoidal condition of fossil Man; next, the stage of acquisition of the bifid character, with reduction of length and angle of inclination; lastly, the stage of retrogression of type until forms reminiscent of lower Primates and other mammalia are reproduced. It would have to be supposed that the bifid forms that occur in the Negroid races are laggards from the second of the stages in the retrograde process. This speculation receives some support from the following considerations. The cleft type

accounts in the Bantus for some 43 per cent. and in the Bushman for two-thirds of all the bifid cervical spinous processes. It will be remembered that earlier (Section IV) arguments were brought forward to support the view that the cleft type is retrogressive. Further, the bifurcate forms, when found in Bantus, conform to the retrogressive "Mediterranean" type in the proportion of almost four-fifths, rather than to the specialised "Nordic" type. Evidently the condition of the cervical spinous processes in the Negroid races in the early stages of their development demands investigation. A full investigation of this sort must be deferred for the present and the findings reserved for a future communication.

I am able, however, to record the following preliminary observations. In the following table the condition of each cervical spinous process if bifid is recorded by the letter B.

Table VII. *The occurrence of bifid cervical spinous processes in Bantu foetuses*

	Estimated age	Vertebra II	III	IV	V	VI	VII	Observer
1.	3 months	—	—	—	B	—	—	N. L. M.
2.	4 „	B	B	B	B	—	—	N. A. R.
3.	4 „	—	B	B	B	B	—	H. S. O.
4.	6 „	—	B	B	B	B	—	N. L. M.
5.	6 „	B	?	?	B	B	—	L. H. W.
6.	7½ „	B	B	B	B	—	—	J. S.
7.	8 „	—	—	B	B	B	B	L. R. S.
8.	8 „	B	?	?	?	—	—	L. H. W.
9.	9 „	—	B	B	B	—	—	L. H. W.
10.	9 „	—	B	B	B	—	—	L. H. W.
Line A		4	6	7	9	4	1	Bantu foetus bifid observed

Table I in Section III gives the following total numbers of cervical spinous processes examined in Bantu skeletons:

Line B	70	67	65	65	70	65	Totals, Bantu adult

Of these the bifid members account for:

Line C	17	9	17	27	15	0	Bifid, Bantu adult

The numbers in Line A, when multiplied by the factor 6·7, which will be explained in the next paragraph, give the following:

Line D	27	40	47	60	27	67	Bifid, Bantu foetus, estimated

Direct comparison is needed between the figures which refer to the incidence of bifid cervical spinous processes in the foetus and in the adult. The totals in Line A refer to 10 foetuses, but those in Line C refer to 71 cervical columns, which, allowing for certain losses, contain an average number of 67 for each unit. When the totals for each vertebra in Line A have been multiplied by the factor 6·7, which is the ratio 67 to 10, inferential values for the bifid cervical spinous processes in the foetus are obtained on the same basis of totality as in

the adult. The numbers in Line C and in Line D now admit of direct comparison. It seems clear that the bifid quality of the cervical spinous processes is more general in the prenatal stages of the Bantu skeleton than in the adult.

It can be presumed that a bifid state precedes the heteromorphous conditions that obtain in the adult Bantu peoples. On the hypothesis of recapitulation, the Bantu as well as the European in the course of evolution has passed through a stage in which the cervical spinous processes were bifid.

XI. SUMMARY AND CONCLUSIONS

The different forms of the cervical spinous processes have been classified in 71 Bantu, 12 Bushman, and 11 European skeletons.

The bifid character of the spinous processes is found in about 71 per cent. of the lower six cervical vertebrae in the European, and in about 7 per cent. in the Bushman. The proportion for the Bantu is about 21 per cent., which is intermediate but nearer to the Bushman.

Bifid spinous processes may have divergent or non-divergent sections. The name bifurcate is given to the first, and cleft to the second type. The cleft type, in all three races, occurs in a smaller proportion than the bifurcate and is considered to be retrogressive.

In the lower six cervical vertebrae the bifurcate type accounts for 51 per cent. of European, 12 per cent. of Bantu and 4 per cent. of Bushman spinous processes.

Differences of form are noted between the bifurcate cervical spinous processes of Nordic and of Mediterranean strains of the Caucasian race. The Mediterranean form is more common in Bantu skeletons.

Non-bifid spinous processes are the rule in Bantu and Bushman cervical columns. Four different types are met with, one of which is peculiar to the seventh vertebra in Europeans, but tends to spread up the cervical column in the Bantu and the Bushman. The same forms occur in Bantu and Bushman skeletons and afford no reliable means of differentiating the two races.

Size is the most reliable criterion for distinguishing Bantu and Bushman cervical vertebrae. Material selected by the two criteria of size and cranial form, in order to obtain the purest Bushman types, shows that there is no single type of cervical spinous process characteristic of the Bushman.

A variety of forms of the spinous process of the axis are described. Some evidence of bisection was found in all the European, in 53 out of 70 Bantu and in 6 out of 9 Bushman specimens. Anomalous forms are commoner in the Bantu axis than in the European, but, in proportion, far the most common in the Bushman; counterparts can be identified in sub-human Primate forms.

The angle of inclination of the spinous process with the body of the cervical vertebra does not differ very materially in the European, Bantu and Bushman races of Man; but all of these contrast with fossil Man and with the anthropoid in the angle of inclination and also in the length of the cervical spinous pro-

cesses. The cervical column of the Bushman may present a primitive feature in a cephalad slope of the second and third spinous processes. Comparative Anatomy shows that the chief variants of the non-bifid cervical spinous processes in the Negroid races reproduce anthropoid, sub-anthropoid and sub-Primate conditions. Bifid cervical spinous processes are peculiar to Man among Primates, and the bifurcate type is mainly characteristic of the Caucasian race of Man.

The evidence of palaeontology, both in Europe and in Africa, shows that primitive Man possessed non-bifid cervical spinous processes. The inference is that the bifid character is an acquisition of a post-primitive epoch.

Observations on the development of the cervical spinous processes by Von Eggeling are reviewed in conjunction with the findings on the skeletons of both European and Negroid races. The evidence of ontogeny suggests that the bifid character of the cervical spinous processes is in a phase of recession in the European. A process of replacement of bifid by non-bifid forms has been initiated.

A few observations on Bantu foetuses show that the cervical spinous processes present a bifid type in the prenatal stages of development more commonly than in adult life. The bifid forms in Bantus are replaced in later life by non-bifid forms which are reminiscent of those of lower mammalia. This replacement is more complete in the Negroid races than in the European.

XII. ACKNOWLEDGEMENTS

I have already expressed my indebtedness to the Curators of the Macgregor Museum, Kimberley. The skeletons on loan to the Anatomy Department of the University of the Witwatersrand have furnished the greater part of the Bushman material that I have examined.

My cordial thanks are due to Mr J. H. Gear, of this University, for furnishing me with information as to the forms of the crania belonging to the Bushman skeletons whose cervical vertebrae I have been examining.

Mr L. H. Wells has very kindly investigated the condition of the cervical spinous processes in certain Bantu foetuses, and in giving me his results, desires me to make acknowledgements to the authorities of the Bridgman Memorial Hospital for permission to make these investigations in the post-mortem room. The members of the 1930 Anatomy B.Sc. class also have given me material help in the same part of the investigation. I am glad to acknowledge my indebtedness.

Dr W. L. H. Duckworth of Cambridge gave me valuable advice and assistance when he referred me to the writings of Von Eggeling, which are unobtainable in Johannesburg. I was thus able to turn my studies in a profitable direction during a recent short visit to England.

Finally, I wish to acknowledge the helpful advice and criticism which have been so kindly and freely given by Prof. R. A. Dart in the course of this investigation.

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A CASE OF CONGENITAL ABSENCE OF THE RADIUS IN A WOMAN AGED 38

By CECIL P. G. WAKELEY, F.R.C.S. (Eng.), F.R.S. (Edin.)
Surgeon to King's College Hospital, and the Belgrave Hospital for Children. Lecturer in Anatomy, King's College, University of London

Congenital absence of the radius, although well known, is an uncommon condition, especially when unassociated with other congenital defects.

In 1882 Shattock described four cases associated with other congenital defects, in still-born foetuses; Fairbank in 1913, Lackey in 1929, and Grant in 1930, have described cases, all of which had multiple congenital deformities.

Hoffa in his statistical report of 1444 cases of deformities, treated at the Würzburg Clinic, mentions one case only of congenital club hand due to congenital absence of the radius.

In 1924 Kato reported three cases and reviewed the literature up to date. He found that at least 250 cases had been recorded. In the 114 cases he collected Antonelli found the condition twice as common in males as compared with females.

The radial defect is usually associated with other concomitant anomalies found elsewhere in the body. Prognosis in most of these cases is grave, as the degree of anomaly may be so extensive as to make life impossible. Kummel states that the prognosis is always grave, as these patients show a general lack of resistance to disease, a case of 27 years old being the oldest recorded. However, Bertwistle recorded two cases, one a young man aged 17, and the other a man aged 30. The case which I am about to describe, that of a married woman aged 38, is probably the oldest case yet recorded.

As a rule, these cases of congenital absence of radius exhibit similar features. The thumb, together with its metacarpal bone, is absent. The limb is affected with general atrophy, and the joint movements are unduly limited.

Treatment is rarely undertaken in these cases, but Albée of New York records an interesting case of a girl aged 12 years, in which the condition was bilateral. He operated, and removed a bonegraft from the girl's tibia, and fixed it into the carpus below, and a prepared notch in the ulna above. After the graft had thoroughly united with the carpus and ulna, an osteotomy was done on each ulna to correct the marked ulnar deviation. He obtained a good result, and a straight forearm.

The following is the history of the case which came under my notice: Mrs Elizabeth M., aged 38, came under observation as the result of a mixed tumour of her palate, which was easily removed under a general anaesthetic. Her right arm, forearm and hand were quite normal, both on clinical and X-ray

Fig. 1.

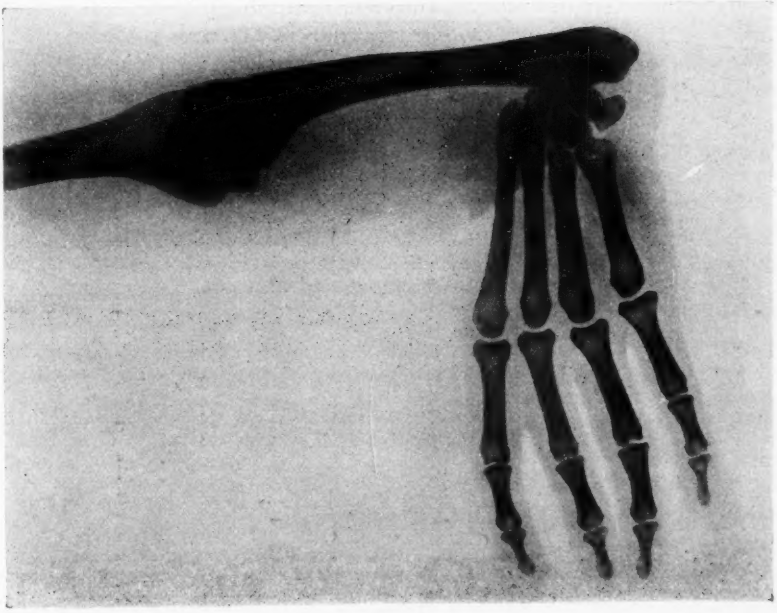

Fig. 2.

examination. On the left side, however, there was congenital absence of the radius with absence of the thumb. The humerus was shorter, and the ulna much smaller than on the right side; and the hand articulated with the distal outer border of the ulna (fig. 1). The lower end of the ulna was prominent, presenting a sort of heel, and an adventitious bursa had formed over it. The index and middle fingers were fused at their bases, and did not enjoy so much freedom of mobility as the ring and little fingers. The hand was held in a position of full pronation, slight supination was possible, and almost full supination could be obtained with assistance. Movements at the elbow joint were free, but flexion was limited to a right angle. There was no wrist joint, but a false joint existed between the lower outer border of the ulna and the cuneiform and pisiform bones; owing to the presence of this pseudarthrosis up and down movements could be made. Flexion and extension of the fingers were by no means complete, but the patient could grip quite well, hold objects in her left hand, and at meal times used a fork very efficiently.

A skiagram (fig. 2) demonstrated the absence of scaphoid, semilunar and trapezium.

A very careful examination was made in this case, to see if any other congenital abnormality was present, but none was discovered. No history of a similar condition could be obtained on either side of the family tree.

Although I have had four cases of congenital absence of radius under my care since the War, this is the only case in which no other congenital abnormality or defect was present. The other interesting points in this case are the age and sex of the patient. The great majority of cases are males, and I cannot find any reference to a published case as old as my patient.

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CONCERNING THE MOUTH OPENING AND CERTAIN FEATURES OF THE VISCERAL ENDOSKELETON OF *CEPHALASPIS*

By EDWARD PHELPS ALLIS, Jr
Menton, France

In a recent and excellent work on fossil remains of the Ostracoderma found in the Downtonian and Devonian deposits of Spitzbergen, Stensiö (1927) comes to the conclusion that the mouth opening of these craniates was terminal and lay between premandibular arches that were complete and serially homologous with the more posterior arches. There is, however, in the Osteostraci, one of the three subdivisions of these craniates, a well-developed naso-hypophysial canal, and in the recent Cyclostomes and fishes this canal is always associated with the mouth that is not terminal (Allis, 1931). I have accordingly carefully considered the conditions in *Cephalaspis*, which is the one of these Ostracoderms most fully described, and although the mouth opening does certainly there seem to be terminal, a comparison with *Petromyzon* shows this to be incorrect. Furthermore the relations of the thickened dorso-mesial edges of the visceral endoskeleton to the neurocranium seem to favour strongly, if they do not actually establish, my contention that the lateral bounding walls of the myodome and trigemino-facialis chambers of the Teleostomi are of branchial-ray origin. The conditions in this part of the skull of *Cephalaspis*, as described by Stensiö, must therefore be first quite fully reviewed.

The head of *Cephalaspis hoeli* was broad and flat, and the skeleton of the head, as preserved in the fossils, forms the cephalic portion of a so-called cephalic shield which has dorsal and ventral portions and is prolonged posteriorly on to the anterior portion of the trunk. This cephalic portion of the shield has ectodermal and endodermal portions, the former of which was developed wholly within the corium and has dorsally and ventrally presented external surfaces. The ventrally presented surface forms a narrow band which surrounds the oralo-branchial fenestra, to be later described, and is referred to as the ventral rim. The dorsal surface is convex and extends from one side of the head to the other throughout its entire extent. At about the anterior third or two-fifths of its length there is a median so-called nasal aperture, the dorso-posterior portion of which forms the external opening of the nasal capsule and the ventro-anterior portion the external opening of the naso-hypophysial canal. The orbits lie immediately posterior to this nasal aperture, not far from the mid-dorsal line, and as the cephalic shield is here quite broad, this gives to the orbits the appearance of having been crowded towards each other on the dorsal surface of the head, but this is incorrect, for they are

separated from each other by a relatively thick interorbital wall which lodges the anterior portion of the brain.

The endodermal portion of the cephalic shield lies immediately internal to the ectodermal one, closely applied to it and in places directly continuous with it. It is said to have cranial and visceral portions, but they are so completely fused with each other that their limiting lines cannot anywhere be recognised.

The neurocranium is considered by Stensiö to extend from the anterior end of the ethmoidal region to the hind end of the occipital, and the skeletal cranial cavity has the same extent and has chordal and prechordal portions. The floor of the chordal portion is formed by what Stensiö considers to be the homologue of the parachordal plate of recent fishes, and it is traversed its full length by the notochord. In the occipital region the chorda lies in a groove on the ventral surface of this parachordal plate, but in the otic region it becomes entirely enclosed within it and at its anterior end turns rather abruptly upward and ends at the dorso-anterior edge of the plate, that edge forming the dorsum sellae. The prechordal portion of the floor begins at this point and at first descends vertically across the anterior edge of the parachordal plate. At the lower edge of that plate the floor curves antero-ventrally and then antero-dorsally and ends at the antero-ventral end of the median nasal aperture, there lying approximately in the horizontal plane of the dorsum sallae. The prechordal portion of the floor of the skeletal cranial cavity thus forms a deep and uniformly continuous depression, and it is perforated at about the middle of its length by the carotid canals, one on either side. That part of the depression that lies posterior to these canals is considered by Stensiö to have lodged the hypophysis and is called by him the fossa hypophyseos. That part of the skeletal cranial cavity that lies anterior to this fossa is called the ethmoidal chamber. It extends from the floor to the roof of the skeletal cranial cavity and is separated into three portions, a rounded dorso-posterior one which lodged the larger part of the median olfactory organ, a cylindrical ventro-anterior portion which lodged part of the membranous naso-hypophysial canal (pituitary sac, Stensiö), and a narrow intermediate portion which is vertical in position, connects the other two and is considered to have lodged a part of the olfactory organ.

The ethmoidal chamber is said to have been separated from that part of the cranial cavity that lodged the brain by a membrane that was perforated by the olfactory nerves as they ran forward to the olfactory organ. This membrane must therefore have formed the anterior wall of the primitive membranous cranium and it must have been continuous dorsally, laterally and ventrally with the more posterior portions of that cranium. The naso-hypophysial canal was certainly primarily a wholly external space, and it is therefore quite probable that the entire ethmoidal chamber and the ventral portion of the fossa hypophyseos were primarily extracranial and that their bounding walls are in large part, if not wholly, of visceral origin.

On the ventral surface of the neurocranium and extending from the ventro-anterior end of the median nasal aperture to the hind edges of the otic capsules there is a broad but low median ridge which is grooved on its ventral surface to lodge the dorsal aorta, that artery being considered by Stensiö to have been single throughout this part of its extent. At the hind edges of the otic capsules the dorsal aorta perforates the dorsal edge of the post-branchial wall, to be described immediately below. The aortal groove is therefore said to be here converted into a short aortal canal, and posterior to this canal the aorta shifts to the right and acquires a position along the right-hand side of the occipital region. The aortal ridge is considered by Stensiö to be of cranial origin, but the fact that it extends forward beyond the parachordal plate and there lies ventral to the naso-hypophysial canal seems unfavourable to this view.

The limiting lines between the visceral and cranial skeletons are not apparent, as already stated, but it is evident that the visceral endoskeleton of *Cephalaspis* encircles the primitive cranium from its anterior end to the hind edges of the otic capsules, projecting antero-ventrally, latero-ventrally and postero-ventrally from it and forming a continuous band, excepting where perforated by certain foramina. The cranial (dorso-mesial) edges of the antero-ventrally and latero-ventrally directed portions of the skeleton are thickened to such an extent that they practically cover the entire anterior and lateral surfaces of the primitive cranium as far posteriorly as the hind ends of the otic capsules. The external (dorsal) and internal (ventral) edges of these cranial edges of the skeleton are prolonged slightly beyond the intervening portions and fuse completely with the dorso-lateral and ventro-lateral edges of the primitive cranium. A primarily extracranial space is thus enclosed between this skeleton and the primitive cranium, and it is incompletely subdivided into several parts which are, from in front backward, the ethmoidal chamber, the ventral portion of the fossa hypophyseos, the orbits, the jugular canals and the so-called myodomes of Stensiö's descriptions. The cranial edge of the postero-ventrally directed portion of the skeleton is not thickened in this manner and this part of it is perforated by two or three foramina which are traversed by the dorsal aorta, the oesophagus and the truncus arteriosus.

The ventral edge of the visceral endoskeleton is everywhere in contact with the internal surface of the so-called ventral rim of the ectoskeleton, and is of the same width as that surface. The ventral rim, which forms the entire ventral surface of the cephalic portion of the cephalic shield, is thus simply the ventral edge of the visceral endoskeleton covered by a layer of bone of ectodermal origin. The visceral endoskeleton together with the aortal ridge thus form the roof and posterior wall of a large oralo-branchial chamber which is without skeletal floor, opening ventrally through a large oralo-branchial fenestra. In the living condition this fenestra was closed by soft tissue which was protected by dermal scales or plates, and was perforated along the edges of the fenestra by a series of openings. The antero-median one of these per-

forations is called the mouth opening, the others, ten in number on either side, being said to open into branchial pouches that were similar to those in the recent *Petromyzon.*

On the internal surface of the visceral endoskeleton, that is on the roof of the oralo-branchial chamber and the anterior surface of its postbranchial wall there is, on either side of the head, a series of ridges, all of which, excepting the most anterior one, become enlarged at their ventral ends to form septa, each of which is said to lie between two adjacent branchial pouches. The anterior one of these ridges begins at the anterior edge of the aortal ridge and extends antero-latero-ventrally to the ventral edge of the skeleton. It is said to lie between the mouth opening and the first branchial pouch, is apparently without septum, and is called the prebranchial or premandibular ridge. The next five ridges arise from the lateral edge of the aortal ridge and running latero-ventrally and curving posteriorly at their outer ends pass between successive branchial pouches and are there enlarged to form interbranchial septa. The first one of the five, the second one of the entire series, is the mandibular (trigeminus) septum ridge, and the succeeding ones the hyal (facialis), glossopharyngeus and first and second vagus, the latter septum-ridge arising from the aortal ridge approximately at the hind edge of the otic capsule. The remaining four septum ridges lie on the postbranchial wall, are the third to sixth vagus ridges and the seventh to the tenth of the entire series. The seventh and eighth ridges arise from that part of the postbranchial wall that arches over the dorsal aorta and extends from the otic capsule to the dorsal edge of the foramen for the oesophagus, the ninth ridge approaching this same part of the postbranchial wall, and the tenth ridge falling into the ninth near its dorsal end.

Between the premandibular ridges of opposite sides of the head there is a triangular rostral plate which is said to have formed the larger part of the roof of the mouth cavity and, in certain of the Ostracoderms examined, it had on its internal (ventral) surface numerous tubercules that are considered to have represented teeth. The median line of this plate must evidently represent the line along which the morphologically anterior edges of the visceral skeletons of opposite sides of the head have met and fused with each other. Similarly, the median line of that part of the postbranchial wall that lies ventral to the foramina for the oesophagus and truncus arteriosus must represent the line along which the morphologically posterior edges of the visceral skeletons of opposite sides have met and fused with each other in the median line. The tenth septum ridge of either side would therefore apparently represent the entire length of a branchial arch of the Cyclostomean type instead of only the dorsal half of such an arch, as Stensiö concluded. The dorsal ends of the four posterior visceral arches of opposite sides have then simply met and fused with each other dorsal to the oesophagus but ventral to the dorsal aorta, while the more anterior arches meet and fuse with the aortal ridge dorsal to the aorta.

On the internal surface of the roof of the oralo-branchial chamber there are on either side three low and rounded prominences, one beneath and somewhat lateral to the nasal capsule, one beneath the orbit and one beneath the otic capsule. The subnasal one of these three prominences lies between the dorsal ends of the hyal and glossopharyngeus septum ridges, the suborbital prominence between the dorsal ends of the glossopharyngeus and first vagus ridges, and the subotic prominence between the first and second vagus ridges.

Internal to each of the visceral ridges there is considered to have been an efferent artery, and certain of the ridges are more or less grooved along their summits (ventral edges) in order to receive the related artery. The artery related to the premandibular ridge is called the rostral artery, and it and the next three following arteries fall independently into the median dorsal aorta. The next following three arteries, that is those related to the first three vagus ridges, fall independently, with their fellows of the opposite side, into a short median arterial trunk which is called the arteria branchialis efferens communis and is enclosed in a median canal in that part of the postbranchial wall that lies between the otic capsule and the dorsal edge of the foramen for the oesophagus. The remaining three efferent arteries, that is those related to the fourth, fifth and sixth vagus ridges, perforate the postbranchial wall and fall into the subclavian artery, which lies on the posterior surface of the postbranchial wall and is assumed by Stensiö to have arisen from the hind end of the arteria branchialis efferens communis. The canal that lodges the latter artery lies between the thickened dorso-mesial edges of the related portions of the visceral endoskeletons of opposite sides of the head, each half of this canal thus seeming to be a space which is serially homologous with the orbit, jugular canal and so-called myodome of its side.

The carotid artery of either side is considered to have arisen from the median dorsal aorta between the points where the latter is joined by the dorsal ends of the efferent arteries of the hyal and glossopharyngeus septum ridges. Running upward it traverses its canal at the anterior edge of the fossa hypophyseos, and while traversing it, or immediately afterwards, separates into two parts, the arteriae facialis and carotis interna. The facialis is distributed in the ethmoidal and orbital regions and does not enter the cranial cavity proper. The internal carotid first runs upward along the lateral surface of the membranous naso-hypophysial canal and must then traverse the membrane that forms the anterior wall of the primitive membranous cranium in order to enter the primitive cranial cavity. In this part of its course it gives off a branch which runs outward with the nervus opticus and is called by Stensiö the arteria ophthalmica magna, but would seem to be the homologue of the arteria centralis retinae of recent fishes.

The orbit of either side is a pit which opens on the dorsal surface of the cephalic shield and from there extends ventrally and somewhat posteromesially in the endoskeleton, its bounding walls being partly of cranial and partly of visceral origin. In its mesial wall there is a large so-called optic

fenestra which extends from the floor of the prechordal portion of the skeletal cranial cavity nearly to its roof and is considered to have been closed throughout its entire extent by membrane. The dorsal portion of this fenestra must have opened directly into the primitive cranial cavity and was probably traversed by the nervi opticus, oculomotorius and trochlearis, as it is in recent fishes. The ventral portion of the fenestra opens directly into the fossa hypophyseos but was quite certainly separated from it either by cartilage or membrane, and the ventral portion of the fossa must have been separated from the primitive cranial cavity by membrane that formed part of the primitive membranous cranium. The ventral portion of the skeletal fenestra was therefore not properly a part of a fenestra optica. The floor of the fossa and those of the orbits lie approximately in the same horizontal plane, and a pituitary vein could easily have passed from one orbit to the other through the fossa. This, however, seems highly improbable, for the pituitary vein of recent fishes always falls into the vena capitis media and that vein is wholly wanting in *Cephalaspis*.

In the postero-ventro-mesial corner of each orbit there is a large fossa, called by Stensiö a wide canal, which is said to extend mesially and in some specimens slightly posteriorly in the floor of the cranial cavity, slightly posterior to the dorsum sellae. It is said to lie in the parachordal plate, but this is true only of its ventro-mesial portion, the dorso-lateral portion lying in the lateral wall of the cranium, as shown in figures of transverse sections through this region and as definitely established by the course of the trigeminus and profundus nerves to be described immediately below. It is considered to have given insertion to certain of the recti muscles and is therefore called by Stensiö the myodome. In certain specimens, these so-called myodomes of opposite sides are said to meet and fuse with each other in the median line dorso-posterior to the turned-up anterior end of the notochord. The canal so formed is considered by Stensiö to be the homologue of the canalis transversus of the Selachii notwithstanding that it lies dorso-posterior to the turned-up anterior end of the notochord, instead of ventro-anterior to it. This canal is not considered by Stensiö to have been traversed by the pituitary veins, as will later appear, but it together with the so-called myodomes of opposite sides are nevertheless considered to form a chamber which is the homologue both of the anterior portion of that part of the myodome of *Amia* that lies beneath the prootic bridge and the corresponding portion of the dorsal compartment of the myodome of the Teleostei.

From the dorso-lateral portion of the so-called myodome of either side several canals lead directly into the cranial cavity, for there is said to be, in most of the specimens examined, no slightest indication of a trigemino-facialis recess in the lateral wall of the cranial cavity. These several canals, with a single exception, are said to have given passage to the roots of the nervi profundus, trigeminus and abducens, and as the roots of the first two mentioned nerves always, in recent fishes, issue from the cranial cavity dorsal to

the parachordal plate, that part of the so-called myodome into which they enter must lie morphologically dorsal to the level of the latter plate. The nervus abducens is said to issue from the cranial cavity with one of the roots of the trigeminus, and the ganglia of the latter nerve and the profundus are said to lie partly in the so-called myodome near its orbital opening, and partly on the floor of the orbit immediately beyond that opening. The one canal considered not to have been traversed by these several nerve-roots is said by Stensiö to have probably given passage to the pituitary vein. That vein did not accordingly traverse the canalis transversus of his descriptions, traversing instead the lateral wall of the cranium and entering the cranial cavity dorsal to the parachordal plate and considerably posterior to the pituitary fossa. This seems to be an impossible course and position for a pituitary vein, and as it is also improbable that, as above explained, this vein passed from one orbit to the other through the fossa hypophyseos, it seems quite certain that the pituitary region was drained by intracranial veins as it is in the recent *Amiurus* (Allis, 1908) and *Petromyzon* (Allis, 1924). The canal through the cranial wall that is considered by Stensiö to have been traversed by the pituitary vein might therefore have given passage to the nervus abducens.

The so-called myodome of *Cephalaspis* thus has none of the characteristic features of the myodome of recent fishes, but it closely resembles the trigeminus part of the trigemino-pituitary fossa of *Acanthias* (Allis, 1914) and the trigeminus fossa of *Polypterus* (Allis, 1922), excepting in that the jugular canal of *Cephalaspis* begins in the hind wall of the orbit somewhat dorso-lateral to the trigeminus fossa, instead of in the posterior wall of that fossa, as it does both in *Acanthias* and *Polypterus*. That part of the fossa (so-called myodome) of *Cephalaspis* that in certain specimens fuses with its fellow of the opposite side dorsal to the notochord, would therefore not be a canalis transversus, but would resemble that part of the trigemino-pituitary fossa of *Chlamydoselachus* that lies between the parachordal cartilage and the tough lining membrane of the cranial cavity and gives insertion to a part of the rectus externus muscle (Allis, 1914, 1923).

The nervus facialis, the preotic lateralis fibres and the fibres destined to innervate the so-called electric fields are all considered to issue from the cranial cavity with the nervus acusticus and enter the labyrinth cavity. There a ganglion forms on the facialis fibres, on the lateralis fibres associated with the facialis and on the electric-field fibres, and from it the truncus facialis and the electric-field nerves have their origins and traverse the dorsal and lateral walls of the otic capsule. The remaining lateralis fibres do not enter this ganglion, but traverse a foramen in the anterior wall of the capsule and enter the orbit, where a ganglion is formed which lies immediately lateral to the trigeminus ganglion.

The nervus profundus, called by Stensiö the ramus ophthalmicus profundus, after issuing from its ganglion is considered by him to have traversed the orbit

dorsal to the nervus opticus. At the anterior end of the orbit it entered a canal that runs antero-ventro-laterally in the visceral endoskeleton and, crossing the lines of the glossopharyngeus, hyal and mandibular septum-ridges, opens into the oralo-branchial chamber slightly anterior to the latter ridge. From there a groove continues the line of the canal, and as it is considered by Stensiö to have been closed by membrane, the nerve actually entered the oralo-branchial chamber slightly posterior to the premandibular ridge which it accompanied in its further distribution. A bundle of lateralis fibres, called by Stensiö the ramus ophthalmicus lateralis, is said to arise from the lateralis ganglion at the hind end of the orbit and to join and fuse completely with the profundus nerve.

The nervus trigeminus, after issuing from its ganglion, is said to receive a bundle of lateralis fibres which arises from the lateralis ganglion and is called by Stensiö the ramus buccalis lateralis. The nerve so formed traverses the orbit and enters a canal that begins in its lateral wall and, running antero-ventro-laterally in the visceral endoskeleton, crosses the lines of the glosso-pharyngeus and hyal septum-ridges and opens in the oralo-branchial chamber between the latter ridge and the mandibular septum-ridge. From there the canal is prolonged forward by a groove closed ventrally by membrane, the nerve definitely entering the oralo-branchial chamber slightly posterior to the mandibular septum ridge and being distributed to the mandibular arch.

The nervus facialis, after issuing from the otic capsule, enters a canal in the visceral endoskeleton which crosses the lines of the first vagus and glosso-pharyngeus septum ridges, and the nerve, after issuing from it into the oralo-branchial chamber, is distributed to the hyal arch.

These several nerves of *Cephalaspis* thus have the same general relations to the orbit and the otic capsule that the corresponding nerves of the recent Cyclostomes and fishes have, but the visceral arches to which they are distributed have shifted relatively quite far forward, for the otic capsule of *Cephalaspis* lies between the dorsal ends of the first and second vagus visceral arches, while the capsule of recent fishes lies approximately between the dorsal ends of the mandibular and hyal arches. The mesial (internal) edge of the hickened dorso-mesial end of the visceral endoskeleton of *Cephalaspis* has accordingly shifted forward relatively to the primitive cranium, the lateral (external) edge being prevented from doing so by the eyeball. The lateral portion of the postorbital process has accordingly been carried forward beneath the eye, and there forms the lateral bounding wall of the orbit, and the nerves have become enclosed in canals that lie in the visceral skeleton morphologically between the mesial and lateral edges of its thickened dorso-mesial end.

The vena capitis lateralis of *Cephalaspis* is said by Stensiö to arise superficially on the rostrum and in the ethmoidal region, to run posteriorly through the orbit and then enter and traverse the jugular canal, which lies between the lateral surface of the otic capsule and the diverging lateral and mesial edges of the dorso-mesial edge of the visceral endoskeleton. The orbital opening

of the canal lies high in the orbit, and hence necessarily dorsal to the trigeminus fossa (myodome, Stensiö), and the vein in this part of its course lies dorsal to the ganglia of the related lateralis nerves. The posterior opening of the canal lies on the posterior surface of the otic capsule, and the jugular vein, after issuing through it, passes dorsal to the ganglion of the nervus glossopharyngeus and then turns ventrally posterior to it, between it and the vagus ganglion, and falls into the anterior end of the vena cardinalis anterior. As this vein of *Cephalaspis* runs posteriorly along the lateral surface of the otic capsule, it has to that capsule and the thickened dorso-mesial edge of the visceral endoskeleton the relations that the vein of the Teleostomi has to the otic capsule and the hyomandibula. As it traverses the hind end of the orbit, Stensiö considers it probable that it received a pituitary vein, that vein issuing from the cranial cavity into the trigeminus fossa (myodome, Stensiö) and then running upward to fall into the vena capitis lateralis. This, however, seems improbable, as already explained, for in the recent gnathostome fishes the pituitary vein always falls into the vena capitis media and not into the vena capitis lateralis.

The vena capitis media, if present, must have run posteriorly in the oralobranchial chamber immediately beneath its roof and then have passed either through the foramen for the dorsal aorta or through that for the oesophagus, for there is no special foramen in the postbranchial wall that could have given passage to it. Because of this, Stensiö concludes that the vena cardinalis anterior of the adult did not extend forward beyond the point where it is joined by the vena capitis lateralis, the vena capitis media thus being completely suppressed. There is no foramen or canal in the roof of the oralobranchial chamber that could have given passage either to a pituitary vein or to a communicating branch from the vena capitis media to the vena capitis lateralis.

DISCUSSION AND COMPARISON

The visceral endoskeleton of *Cephalaspis* is considered by Stensiö to be the homologue of the cartilaginous visceral skeleton of *Petromyzon*, and the bars of the branchial basket of the latter Cyclostome to be the homologues of the branchial bars of the Gnathostomata. The latter homology is now, I believe, the generally accepted one, but certain statements by Russian authors seem unfavourable to it and may be here referred to.

Krivetsky (1917) says that there is but one mesodermal segment in the hyal arch of those of the Batoidei that he examined, but that the bar of the arch has separated into two distinctly different parts which lie somewhat apart from each other. The inner branchial bar of the arch, which Krivetsky considers to consist of an epihyal and a hyoideum, is carried forward in connection with the development of the transversely placed opening of the mouth. The epihyal then becomes the hyomandibula, but the hyoideum (ceratohyal)

is reduced to ligament or to ligament associated with one or more rudimentary bits of cartilage. The branchial rays of the arch, which were primarily related to and attached to the epal and ceratal elements of the arch, were left behind, as the inner bar shifted forward, because of their attachment to the anterior surface of the hyobranchial gill-pouch, and they became what Krivetsky calls the pseudohyoideum. This pseudohyoideum has been heretofore considered (Gegenbaur, 1872) to be the primarily ventral half of the hyal arch somewhat displaced in position, and it separates into two parts which Parker (1876) calls the epihyal and ceratohyal. These latter two parts of the arch have the appearance of being serial homologues of the corresponding elements of the branchial arches and hence parts of an inner branchial bar, but Krivetsky considers that their branchial-ray origin is definitely established by the fact that the commissural vessel between the anterior and posterior efferent arteries of the arch passes internal instead of external to them. A hypohyal is shown by Parker attached to the ventral end of the pseudoceratohyal. The epihyal of these descriptions is in my opinion the pharyngohyal (Allis, 1915, etc.). If this be correct and if Krivetsky's observations are accepted, comparison with the conditions in the adult *Raia* and *Torpedo* would strongly suggest that inner branchial bars that corresponded to the epal and ceratal elements of the branchial bars of the Plagiostomi might be developed from preexisting branchial rays that formed a branchial basket resembling that of *Petromyzon* and, like that basket, was not primarily attached to the axial skeleton. Such a basket is considered by Woskoboynikoff (1909) to have been the primitive condition in all vertebrates. I have been unable to consult the works of the latter author, but Sewertzoff makes frequent reference to them and as certain features in the later development of the branchial arches, as given by him, are important they may here be referred to. It will, however, be best first to summarise briefly certain of Sewertzoff's statements regarding his own observations on the development of the visceral arches of *Petromyzon*.

According to Sewertzoff (1916, 1917) the visceral bars of *Petromyzon* first appear as short rods of cartilage, one in each arch, and he considers this to represent the primitive condition for all vertebrates. Those of these bars that are related to the branchial arches are said to later grow dorso-antero-mesially and ultimately meet and fuse with the bar of the next anterior arch, the bar of the first branchial arch meeting and fusing with the lateral surface of the posterior portion of the parachordal. This end of each bar is called by Sewertzoff the anterior subchordal cartilage, and somewhat later a posterior subchordal cartilage develops as a process of the bar but in a mass of mesoderm that was primarily somewhat independent. It completely disappears in the adult. In the hyal arch anterior and posterior processes develop, similar to those in the branchial arches, but the posterior process is primarily a wholly independent cartilage. The anterior process fuses with the distal end of a process of the anterior parachordal that Sewertzoff considers to form the dorsal end of the bar of the mandibular arch, the posterior process fusing with the hyal bar

and forming its dorsal end, that end of the bar therefore being directed posteriorly instead of, as in the branchial arches, anteriorly. The little process of the parachordal that Sewertzoff considers to represent the dorsal end of the mandibular bar, is said to be the stylohyal of earlier authors. It has approximately the relations to the mandibular bar that the posterior process of the hyal arch has to the bar of that arch, and the relations to the nerves, arteries and veins of the region that the processus basipterygoideus of the Teleostomi has. The dorsal end of the mandibular bar fuses with it, and they together form the posterior boundary of the fenestra suborbitalis, the anterior boundary of that fenestra being formed by what Sewertzoff considers to be the bar of the premandibular arch.

Woskoboynikoff (1909) is said by Sewertzoff to consider the epal and ceratal elements, alone, of the branchial bars of the Gnathostomata to correspond to the entire bars of the branchial basket of *Petromyzon*. Branchial rays are developed in relation to the bars of the Gnathostomata, but nothing is said as to whether these rays and bars correspond to the branchial bars and rays of the Plagiostomi or to those of the pseudobranchial bar of the hyal arch of the Batoidei. A process directed dorso-antero-mesially in the line prolonged of the epal element is said to be developed on the dorsal end of that element, and I have described it in the adults of the Teleostomi (Allis, 1925). It does not occur in the Plagiostomi, so far as I could find, and as it lies ventral and anterior to the efferent artery of its arch, it would seem not to be the homologue of the anterior subchordal process of Sewertzoff's descriptions of *Petromyzon*. The bars of the branchial arches are said by Woskoboynikoff not to have been primarily attached to the axial skeleton, but this attachment is later acquired by the development of pharyngeal elements from the dorsal one of the branchial rays related to each arch. It is not said whether this applies to the infrapharyngobranchials of the Teleostomi or to the suprapharyngobranchials, but as there are two rows of branchial rays in each arch of these fishes it is possible that it applies to both of them, the one lying anterior to the efferent artery of the arch and the other posterior to it. In the Plagiostomi, where there is but a single row of branchial rays, there is but a single pharyngeal element. In *Petromyzon* the suprapharyngobranchial is apparently represented in the posterior subchordal process of Sewertzoff's descriptions.

If the suprapharyngeal elements of the branchial arches and possibly also the infrapharyngeal elements, are of branchial-ray origin, as above suggested, it is evident that the corresponding elements of the prebranchial arches must be of similar origin. The hyomandibula, the lateral wall of the trigeminofacialis chamber and the pedicel of the alisphenoid of the Teleostomi would then be, respectively, the suprapharyngeal elements of the hyal, mandibular and premandibular arches, and the polar and trabecular cartilages the infrapharyngeal elements of the mandibular and premandibular arches. In the Plagiostomi, if the pharyngeal elements are of branchial-ray origin, it must be assumed that it is the ventral ends of the branchial rays, and not their dorsal

ends that have acquired attachment to the axial skeleton. In *Cephalaspis*, the thickened dorso-mesial edges of the visceral endoskeleton would be of branchial-ray origin and the floor of the prechordal portion of the cranium would be formed wholly or in part by bars of cartilage that are the homologues of the trabecular and intertrabecular cartilages of *Petromyzon*, the trabeculae of the latter Cyclostome probably being the homologues of the trabeculo-polar bars of the Teleostomi.

Mouth opening

The mouth opening of *Cephalaspis* is considered by Stensiö to have lain at the antero-median edge of the oralo-branchial fenestra, between the pre-mandibular visceral arches of opposite sides of the head. Between the pre-mandibular and mandibular arches of either side there is said to have been a gill pouch which was the serial homologue of the more posterior pouches, but lined with ectoderm instead of endoderm. The velar fold, if present, is said to have lain between the mandibular arches of opposite sides of the head.

The mouth opening of *Cephalaspis* is thus considered by Stensiö to have been terminal, and as the Ostracoderms are said to have been closely related to the ancestors of the recent Cyclostomes, it seems quite certain that Stensiö considers the mouth opening of *Petromyzon* also to be terminal. This cannot, however, be if Kupffer's descriptions and figures of *Petromyzon* (1894) and *Bdellostoma* (1900) are correct, for the bucco-pharyngeal opening, which leads from the alimentary canal into the stomodaeum, is there shown lying in the floor of the alimentary canal definitely posterior to the anterior end of the canal (Allis, 1931). Sewertzoff is, however, also of the opinion that the mouth opening of *Petromyzon* is terminal, and his descriptions must be considered.

According to Sewertzoff (1916, 1917) the velar fold of embryos of *Petromyzon* lies between the mandibular arches of opposite sides of the head, but the alimentary canal extends forward beyond this fold and ends at the external opening of the mouth. The velar fold is generally considered to be developed in what remains of the bucco-pharyngeal plate after that plate has broken through to form the bucco-pharyngeal opening. The bucco-pharyngeal plate primarily lay between the alimentary canal and the stomodaeum, completely separating them from each other, the stomodaeum being a wholly external space secondarily enclosed between outgrowths of the bounding edges of the plate. It later becomes the buccal cavity, which is thus primarily lined with ectoderm throughout its entire extent. Three little rods of cartilage are said by Sewertzoff to develop, on either side of the head, in the walls of this cavity and he considers them to be the bars of three complete premandibular visceral arches. Between the posterior one of these three rods and the bar of the mandibular arch there is said to be, on either side, an evagination of the lateral wall of the buccal cavity, and Sewertzoff considers it to be a rudimentary premandibular visceral cleft serially homologous with the more posterior ones, but lined with ectoderm instead of endoderm. This ectoderm is said to be an

ingrowth of the external lining of the head that has secondarily invaded the cavity through the mouth opening and Stensiö makes a similar statement regarding the ectodermal lining of the premandibular portion of the oralo-branchial chamber of *Cephalaspis*.

Similar conditions to those above described in *Petromyzon* are considered by Sewertzoff (1925) to exist also in embryos of *Acanthias* and *Pristiurus*, for he says that the alimentary canal is there prolonged beyond the mandibular arches to the external opening of the mouth. This so-considered anterior prolongation of the alimentary canal is certainly simply the stomodaeum, and Sewertzoff refers to it both as the buccal cavity and the pharynx. Two complete premandibular visceral arches are described in the walls of this cavity, instead of three, as in *Petromyzon*, and the bars of these two arches are considered to be represented in the anterior and posterior labial cartilages of current descriptions of the adult.

Sewertzoff and Stensiö thus both consider the mouth to be terminal in *Petromyzon*, and Sewertzoff considers it to be terminal also in the Selachii. This cannot, however, be if v. Kupffer's (1893, 1894, 1900), Scammon's (1911) and Haller's (1923) descriptions and figures of certain of the Cyclostomes and fishes are correct. According to these latter authors, the anterior end of the alimentary canal lies at the anterior end of the preoral gut, the bucco-pharyngeal opening lies posterior to that gut, and the external opening of the mouth is the external opening of the stomodaeum. The rods of cartilage that are considered by Sewertzoff to be the bars of premandibular arches cannot therefore be the homologues of the bars of the more posterior arches and they must be developed in tissues that have been carried forward into the walls of the stomodaeum (buccal cavity) as those walls developed, and they must have been derived from the mandibular or premandibular mesodermal arches and probably be of branchial-ray origin. The so-called premandibular ridge of *Cephalaspis*, which must be the homologue of certain of these little bars of *Petromyzon* and the Plagiostomi, cannot therefore represent a typical visceral arch, and the arteries, nerves and muscles of the region are favourable to this view, as will later appear.

Arteries

The bucco-pharyngeal opening of the recent Cyclostomes and fishes lay primarily, as already stated, in the floor of the alimentary canal, between the ventral ends of the mandibular and premandibular visceral arches. The truncus arteriosus, as it ran forward, must therefore necessarily have become double when it reached the hind edge of this opening, each lateral half of the truncus running forward along the lateral edge of the opening until it reached the ventral end of the premandibular arch where it turned upward in that arch to form the premandibular aortic arch. The bucco-pharyngeal opening later became tilted upward and forward in connection with the suppression of the premandibular section of the alimentary canal and the marked ventral

growth of the mandibular arches. This carried each lateral half of the truncus arteriosus upward and forward into a position parallel to and but slightly anterior to the mandibular aortic arch of its side of the head. When, in *Petromyzon* and *Cephalaspis*, the Cyclostomean upper lip was developed, each premandibular lateral half of the truncus arteriosus was carried forward in it, and together with the premandibular aortic arch formed the afferent and efferent premandibular branchial arteries. In the Gnathostomata, where the Cyclostomean upper lip is not developed, each lateral half of the truncus arteriosus must necessarily either have become reduced or have fused with the mandibular artery, the premandibular aortic arch arising from the so-formed artery near its dorsal end and apparently being in some part represented by the arteria ophthalmica magna.

Nerves

The only nerves of *Cephalaspis* it is necessary here to consider are the preotic lateralis nerves and the so-called ramus ophthalmicus profundus of Stensiö's descriptions, and as his conclusions regarding these nerves are evidently based on the descriptions of the nerves in *Petromyzon*, the conditions in the latter must first be carefully considered.

According to Johnston (1905), all of the preotic lateralis fibres of *Petromyzon* issue from the cranial cavity with the nervi facialis and acusticus and enter the labyrinth cavity, where a ganglion immediately forms on the general cutaneous and communis fibres of the facialis. The lateralis fibres run downward closely applied to this ganglion, but enclosed in a membranous sheath derived from the membranous wall that separates the cranial and labyrinth cavities. The truncus facialis arises from the intracapsular ganglion and, joining the lateralis fibres, issues with them through a foramen that perforates the antero-mesial corner of the floor of the capsule, a ganglion then immediately forming on the lateralis fibres. This latter ganglion has posterior and anterior divisions which lie, respectively, on the ventral and antero-ventral surfaces of the otic capsule and are connected by a strand of tissue which is partly fibrous and partly ganglionic. The truncus hyomandibularis and related lateralis fibres arise from the posterior division of this ganglion. From the anterior division three nerves are said to arise:

1. A ramus communicans VII–X, the proximal portion of which is considered to correspond to the ramus oticus lateralis of the Gnathostomata.

2. A ramus buccalis, which is said to run forward dorsal to the rami maxillaris and mandibularis trigemini and innervate the organs of a latero-sensory line which is considered to represent the entire suborbital line.

3. A ramus ophthalmicus superficialis VII which is joined by a ramus ophthalmicus superficialis V, the nerve so formed joining and fusing so completely with the so-called ramus ophthalmicus profundus that the fibres of the three nerves cannot be further separately traced. From this so-called

ramus ophthalmicus profundus a branch is said to be sent forward beneath a line of latero-sensory organs that is considered to form the anterior division of the supraorbital line, and Johnston considers that this nerve innervates this line of organs and that the fibres that compose it are derived from the so-called ramus ophthalmicus superficialis VII.

The so-called ramus ophthalmicus profundus, as it issues from its ganglion, is said by Johnston to be composed entirely of general cutaneous fibres, but certain of the fibres of the root of the nerve have their origin in the acusticum and are hence considered to be lateralis. These lateralis fibres are said to issue from the profundus ganglion as an independent nerve which runs dorsally close against the lateral wall of the neurocranium and innervates certain organs on the dorsal surface of the head which are considered to form the posterior division of the supraorbital latero-sensory line. This nerve, as it runs upward, is shown (Johnston, 1905, p. 152, fig. 1) lying internal to a large venous sinus which lies internal to the ventro-mesial corner of the dorsal division of the musculus capitis lateralis and is probably the vena capitis lateralis of current descriptions. This origin and course of this lateralis nerve seeming to me to be exceptional and, furthermore, doubting the association of lateralis fibres with a true ramus ophthalmicus profundus, I endeavoured some years ago to trace these nerves in serial sections that I have of *Entosphenus tridentatus*. These sections proved unsatisfactory for this purpose, for no fibres of the nerves could be definitely traced to any of the organs of the so-called two divisions of the supraorbital latero-sensory line. Certain of the results obtained may, however, here be presented.

In my specimen of *Entosphenus tridentatus*, the preotic lateralis fibres issue from the cranium with the nervus facialis in the manner described by Johnston in *Petromyzon*, and ganglia develop in relation to them, similar to those in the latter Cyclostome. From the anterior lateralis ganglion four nerves arise:

1. The ramus communicans VII–X which is similar to that of *Petromyzon*.

2. A small nerve which issues from the ganglion close to the base of the ramus communicans VII–X and runs outward in the membranous septum that lies between the dorsal and ventral divisions of the musculus capitis lateralis. When this nerve reaches the level of the outer surfaces of these muscles it turns upward external to the dorsal muscle and could be traced close to two organs that represent the posterior division of the supraorbital latero-sensory line of Johnston's descriptions. The fibres of the nerve could not be traced definitely to these organs, but it seems unquestionable that they were innervated by this nerve.

3. A ramus buccalis lateralis which runs forward dorsal to the rami maxillaris and mandibularis trigemini. It first sends a branch downward to innervate the organs of a line that corresponds to the circumbuccal latero-sensory line of Razzauti's (1916) descriptions of *Petromyzon planeri*, this line of organs not being described by either Alcock (1898) or Johnston (1905). The buccalis then sends branches to the organs of the so-called suborbital line of

Johnston's descriptions, and at the anterior end of that line turns sharply upward and then forward, crosses the external surface of the so-called ramus ophthalmicus profundus closely applied to it, and then continues onward beneath the so-called anterior division of the supraorbital latero-sensory line, lying between that line and the so-called ramus ophthalmicus profundus. No fibres of the nerve could be traced to any of the organs of the latter line, but as the nerve certainly contains lateralis fibres and does not extend beyond the line of organs, it seems certain that they must be innervated by it. Furthermore, Alcock says that in the *Ammocoetes* of *Petromyzon planeri* this line of organs and those of the so-called suborbital line of Johnston's descriptions are all innervated by what she calls the ramus ophthalmicus superficialis, but as this nerve is said to lie between the eyeball and the floor of the orbit, it is evidently a ramus buccalis and not an ophthalmicus superficialis. These two lines of organs thus quite certainly both belong to the suborbital line.

4. A nerve which is immediately joined by a small nerve that arises from the trigeminus ganglion, the nerve so-formed joining the so-called ramus ophthalmicus profundus close to its origin from its ganglion and fusing completely with it. The so-formed nerve runs forward dorsal to the superior division of the nervus oculomotorius and dorsal also to the musculus rectus superior. Its relation to the nervus trochlearis could not be determined, but the profundus fibres of the nerve certainly form a portio ophthalmici profundi such as is found in *Polypterus* and *Acipenser* and not a ramus ophthalmicus profundus, for the latter nerve always lies ventral to the superior division of the nervus oculomotorius. The component of the nerve that is derived from the anterior lateralis ganglion must therefore contain communis instead of lateralis fibres, these communis fibres usually being found associated with general cutaneous fibres in the ramus ophthalmicus superficialis trigemini of the Teleostomi. Neither the portio ophthalmici profundi nor the ramus ophthalmicus profundus of recent fishes contain any motor fibres, and the ramus ophthalmicus profundus is never accompanied by lateralis fibres.

The conditions in *Cephalaspis* may now be considered. According to Stensiö, and as already stated, the trigeminus and profundus ganglia of this craniate must have lain in the so-called myodome near its orbital opening, or on the floor of the orbit immediately beyond that opening. From the trigeminus ganglion a single nerve is said to have arisen, the truncus trigeminus, which ran forward in the orbit ventral to the nervus opticus, entered and traversed the trigeminus canal in the visceral endoskeleton, and having entered the oralo-branchial chamber was distributed to the mandibular arch. From the profundus ganglion a single nerve also arose, the so-called ramus ophthalmicus profundus, which ran forward in the orbit dorsal to the nervus opticus. At the anterior end of the orbit it entered and traversed the profundus canal in the visceral endoskeleton, and having issued from it into the oralo-branchial chamber was distributed to what Stensiö considers to have been a premandibular arch, certain branches going to the rostral region. This

so-called ramus ophthalmicus profundus is considered to have contained motor, general cutaneous, communis and lateralis fibres, and to have been a complete and independent branchial nerve related to a premandibular visceral arch. No such nerve is known in recent fishes, and because of this Stensiö concluded that the conditions in *Cephalaspis* were primitive in this respect and common to the ancestors of all craniates. It is, however, to be noted that Stensiö simply assumes this nerve to have arisen from the profundus ganglion. If it be assumed that it arose from the trigeminus, instead of the profundus ganglion and ran forward ventral to the nervus opticus instead of dorsal to that nerve, it would strikingly resemble the ramus maxillaris trigemini of current descriptions of *Petromyzon*, and as Sewertzoff considers this latter nerve also to be a premandibular one, his description of it must be considered.

Sewertzoff concludes, as already stated, that there were three premandibular visceral arches in *Petromyzon*, each represented on either side of the head by a rod of cartilage that lies in the lateral wall of the buccal cavity. These bars do not therefore occupy positions that are topographically homologous with those occupied by the bars of the more posterior arches, for they lie in the wall of what was primarily the stomodaeum and not in the premandibular portion of the alimentary canal, that part of the canal being represented in the preoral gut of v. Kupffer's (1894, 1900) descriptions of both *Petromyzon* and *Bdellostoma*.

The so-called premandibular bars of Sewertzoff's descriptions are thus, as already stated, quite certainly developed in tissues that have been secondarily carried forward into the walls of the buccal cavity (stomodaeum) as that cavity developed and they apparently might be either of mandibular or premandibular origin. The lateral truncus arteriosus of either side has similarly been carried forward into the related lateral wall of the buccal cavity, as already explained, and it is exceedingly probable that a large part, if not all, of the musculus constrictor superficialis of the mandibular arch has been similarly carried forward into this wall. The ramus maxillaris trigemini which innervates the latter muscle would then simply be a branch of the ramus mandibularis trigemini and not, as Sewertzoff concludes the nerve of a premandibular arch, and the so-called ramus ophthalmicus profundus of Stensiö's descriptions of *Cephalaspis* would be a similar branch of the nervus trigeminus.

CONCLUSIONS

There was in *Cephalaspis* a well-developed naso-hypophysial canal strictly similar in all important respects to that in *Petromyzon*.

Associated with the development of this canal, a premandibular section of the alimentary canal must therefore have been suppressed during ontogeny, as it actually is in *Petromyzon* and in all recent fishes.

The mouth of *Cephalaspis*, like that of *Petromyzon*, was therefore not terminal, the bucco-pharyngeal opening which leads from the alimentary canal into the buccal cavity being a perforation of that part of the floor of the

alimentary canal that lay primarily between the ventral ends of the mandibular and premandibular arches. Later, as the premandibular section of the alimentary canal became suppressed, the bucco-pharyngeal opening and the velar fold, which is developed in relation to it, came to lie secondarily between the mandibular arches of opposite sides of the head.

All that part of the oralo-branchial chamber of *Cephalaspis* that lies anterior to the mandibular visceral ridges must therefore belong to the buccal cavity and form no part of the alimentary canal.

The so-called premandibular visceral ridge of *Cephalaspis* therefore lies wholly in the wall of the buccal cavity, as do also the three so-called premandibular visceral rods of Sewertzoff's descriptions of early embryos of *Petromyzon* and the anterior and posterior labial cartilages of his descriptions of early embryos of the Plagiostomi. These several structures must therefore be developed in tissues that have been secondarily carried forward into the walls of the buccal cavity, and cannot be serial homologues of the visceral bars developed in the walls of the alimentary canal. That the tissues here concerned are of premandibular origin, derived from the premandibular mesodermal arches when the related portion of the alimentary canal became reduced and ultimately suppressed, is quite probable.

The truncus arteriosus of *Cephalaspis* quite certainly ran forward, as it does in *Petromyzon*, until it reached the ventro-posterior edge of the bucco-pharyngeal opening. There it separated into two parts, one on either side of the opening, each of which continued onward until it reached and became continuous with the ventral end of the premandibular aortic arch. As the premandibular portion of the alimentary canal aborted and the hypertrophied upper lip developed, the so-formed arterial trunk was carried forward into the lip, as was also a large part of the musculus constrictor superficialis of the mandibular arch. The artery and the larger part of the muscle become associated, in *Petromyzon*, with the posterior one of the supporting cartilages of the lip and so form with that cartilage what has the appearance of being a complete premandibular visceral arch.

The so-called ramus ophthalmicus profundus of Stensiö's descriptions of *Cephalaspis* is quite certainly the homologue of the ramus maxillaris trigemini of current descriptions of *Petromyzon*, and like that nerve is simply an anterior branch of the ramus mandibularis trigemini, and not in any respect the branchial nerve of a premandibular arch. It is accordingly probable that there was in *Cephalaspis* no ramus ophthalmicus profundus, but a portio ophthalmici profundi not described by Stensiö and apparently composed entirely of communis fibres.

The thickened dorso-mesial (cranial) edges of the visceral endoskeleton of *Cephalaspis* form the lateral bounding walls of the ethmoidal chamber, the orbits, the jugular canals and the so-called myodomes. These edges of the visceral endoskeleton are quite certainly of branchial-ray origin which, if correct, is definite confirmation of my contention that the hyomandibulae, the

lateral walls of the myodomes and those of the partes jugularis of the trigemino-facialis chambers of recent fishes are of branchial-ray origin.

The jugular canal and the so-called myodome of either side apparently form a latero-pituitary space, but while there apparently is a prechordal portion of a subpituitary space there is no subchordal portion and hence no myodome comparable to that in the recent Teleostomi.

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TRANSPOSITION OF THE VENTRICLES AND THE ARTERIAL STEMS

By THOMAS WALMSLEY

Queen's University, Belfast

The heart which is described here is that of a man who died of heart failure at 35 years of age; for at least 10 years previously there had been complete heart block, the pulse rate being about 40 per minute, but until a month before his death the man had followed the fairly heavy work of a cloth-presser[1].

It was noted, during the removal of the heart, that at its commencement the aorta lay in front of the pulmonary artery and that the two vessels ran straight upwards, maintaining their position and without any spiral twisting on one another, to the upper limit of the pericardium. Outside of the pericardium the aortic arch passed backwards over the left pulmonary artery, and from its summit there arose a common stem for the right subclavian artery and the right and left common carotid arteries and, close to it, as a separate vessel, the left subclavian artery. The ligamentum arteriosum was impervious; and the left recurrent laryngeal nerve had its usual relations. There was no transposition of any of the viscera. No notes were made of the position of the heart or of its relation to the chest wall.

The aorta and the pulmonary artery, in this specimen of transposition of the arterial stems, arise, it would seem, from their proper ventricles. The ventricle of the left side is continued upwards anteriorly and on the right into a short infundibular part from which the aorta takes origin (fig. 2); there is no infundibular part of the ventricle of the right side, the pulmonary artery which arises from it arising directly from the ventricular base. At their origin the aorta lies in front and to the left of the pulmonary artery in as nearly as possible a reversal of their usual positions; both orifices are of average size (fig. 1).

The heart is considerably enlarged, especially in its transverse axis, the maximum circumference round the ventricles being 14·75 inches. It is much more rounded in its form than usual, approaching more closely the foetal than the normal adult form; the maximum transverse diameter of the ventricles (d) is 5·7 inches and the maximum ventricular height (h) is 4·6 inches, so that the h/d ratio is 0·8[2]. The margo acutus is replaced by a rounded surface, the

[1] The clinical history, the electrocardiograph findings, and the details of the coronary artery distribution and of the histology of the a.-v. system will be described in a later paper.

[2] See Zimmermann, "Über die Form des Herzens in Abhängigkeit von seiner Arbeit." *Anat. Anz.* Bd. LXIX, S. 466, 1930.

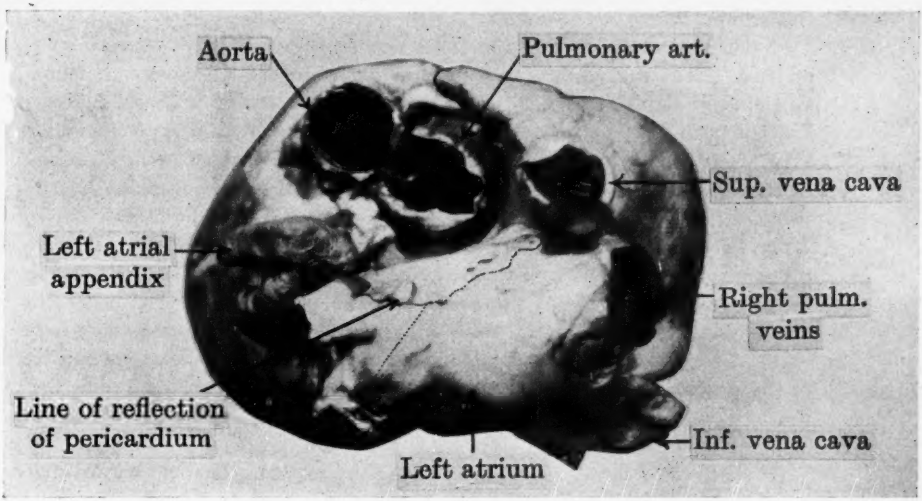


Fig. 1. The heart viewed from above.

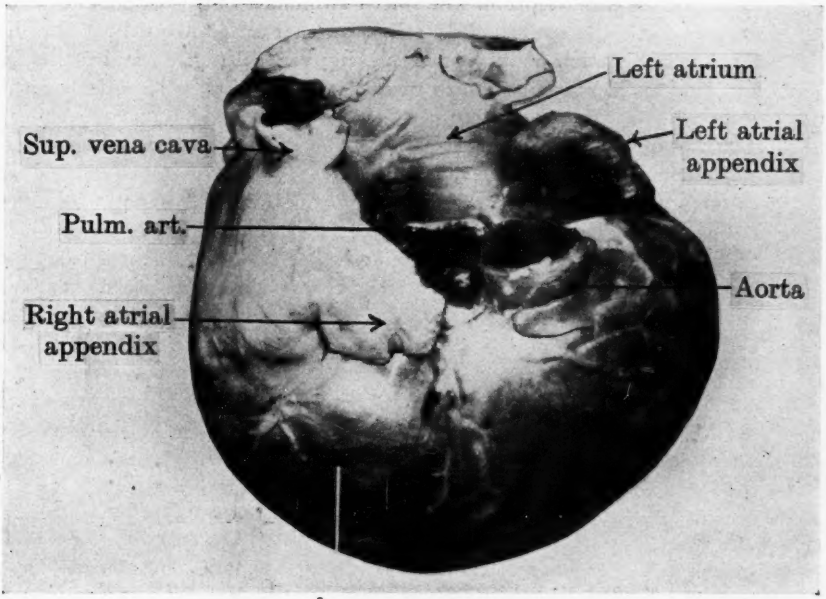


Fig. 2. The heart viewed from in front, above, and the right.

change in the form of the heart being largely due to the alteration in form of this region.

As viewed directly from the front the ventricular region appears symmetrical about the aorta. The anterior inter-ventricular groove commences on the right side of the aorta, runs downwards and to the left, and cuts the lower margin of the heart to the left of its lowest point. The posterior inter-ventricular groove lies in the same relative position, so that the greater part of the ventricular region on both surfaces of the heart is occupied by the ventricle of the left side. The apex of the heart is about the middle of the lower border. The separation between the atria and the ventricles is more pronounced than usual, and when the heart is viewed from the front and in the conventional position, the aorta and the pulmonary artery being cut across above their valves, the anterior surface of the left atrium is more fully exposed than is normal (fig. 2). This is due partly to an increase in the size of the pre-atrial area of the ventricular base, especially on the left side, and partly to a vertical elongation of the atrial chambers, the long axis of both of which is vertical.

The orifice of the superior cava in the right atrium is farther forward than is normal; it lies immediately above the orifice of the atrial appendix (figs. 1 and 7), the crista terminalis alone intervening, and it is separated from the orifice of the inferior cava by the antero-posterior as well as by the vertical extent of the atrial septum. The sulcus terminalis thus runs backwards over the roof of the atrium. The left atrium is remarkable for the alteration in its shape, the direction of its long axis being vertical (fig. 2), and for its large and long atrial appendix which measures 4·75 inches in its axial length; it is the longest atrial appendix which I have seen[1]. The pulmonary veins open into the upper part of the left atrium. The line of the pericardial reflection crosses the front part of the roof (fig. 1).

The arrangement of the arterial cusps in the atrial roots is the normal arrangement[2], and it is possible to identify the divided and undivided bulbar rudiments from which the cusps are derived (figs. 1 and 3). It is to be noted here that the left coronary artery of this heart arises opposite the non-septal cusp of the aortic valve, and, further, that the anterior inter-ventricular artery is a branch of the right coronary artery (fig. 4). The details of the coronary distribution[3] (fig. 4) demonstrate an almost exact reversal of the coronary fields on the front and back of the heart, and also, what is of significance, that the septal arteries, when viewed from behind (fig. 4), run downwards and to the left instead of downwards and to the right; and among them there can be distinguished, as a branch of the anterior inter-ventricular artery as is usual, the artery of the moderator band[4].

[1] See Keith, *J. Anat.* vol. XLVI, p. 211, 1911–12.

[2] See Quain's *Anatomy*, "The Heart," vol. IV, pt. 3, p. 48, 1929.

[3] See p. 528, footnote 1.

[4] Alterations of the origin of the branches of the coronary arteries and in their distribution are common in all types of transposition of the arterial stems, but little attention has been paid

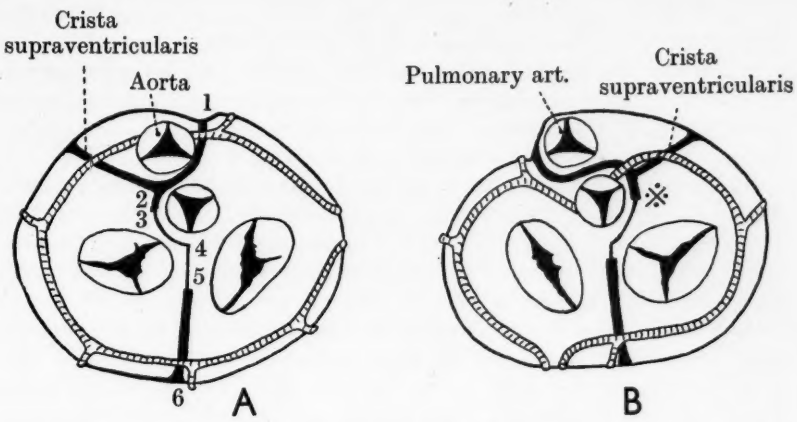


Fig. 3. Diagram to show (*a*) the position of the arterial orifices; (*b*) the position and several parts of the ventricular septum 1–6; (*c*) the arrangement of the cusps of the a.-v. valves; (*d*) the position of the crista supraventricularis; and (*e*) the origin and distribution of the coronary arteries in (A) a case of "corrected transposition" and (B) the normal heart. ※ The position of origin of the right aorta.

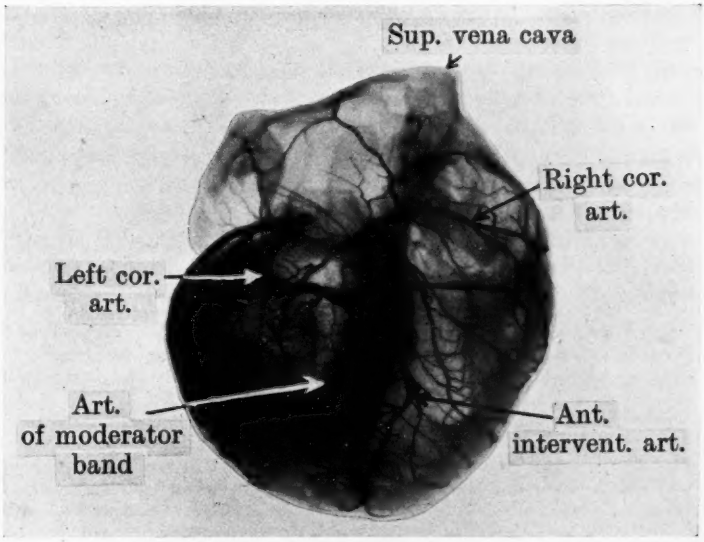


Fig. 4. X-ray photograph of injected coronary arteries in a case of "corrected transposition"; viewed from behind.

The arrangement of the coronary sinus and of the great veins of the heart wall, with the exception of the anterior inter-ventricular vein, is normal. The anterior inter-ventricular vein, which drains the front of both ventricles, turns to the right in the coronary sulcus, and after a short course in it crosses the right coronary artery and enters the right atrium on its lateral side and in front of the sulcus terminalis. No special significance need be attached, I believe, to this mode of termination of this vein for in the normal heart the small cardiac veins of the right ventricle terminate in this manner; but the direction of the stem of the anterior inter-ventricular vein is the reverse of normal and its separation from the coronary sinus may be a factor in the non-emancipation of the orifice of the coronary sinus from the sinus area to the atrial area of the right atrium[1] (*vide infra*).

The atrial and ventricular septa of this heart are complete. The foramen ovale is completely closed and the valve of the foramen ovale, as seen from the left atrium, is of a usual form. There are distinct evidences of the left venous valve in the form of a thin narrow membrane which lies along the septal margin of the inferior cava close to the lower edge of the septum ovale and extends backwards below the posterior limb of the annulus ovalis and forwards below the anterior limb; and from the membrane a rich though fine trabeculated network extends upwards on to the septum ovale. The Eustachian valve is continuous with the Thebesian valve, that is, it does not pass on to the septal side of the caval orifice but is continued straight on below the orifice of the coronary sinus; there is therefore no fold between the orifices of the inferior cava and coronary sinus, and by pulling on the Eustachian valve nothing in the nature of the ridge caused by the tendon of Todaro can be raised. The free edge of the left venous valve can easily be followed on the lower part of the atrial septum above the orifice of the coronary sinus; and by pulling on the common Eustachian-Thebesian valve a number of little ridges are raised which pass below the coronary orifice and join the remains of the left venous valve. The lower part of the sinus area can thus be readily defined and in it there is the orifice of the coronary sinus[2].

to them and their classification seems hardly possible; but though in "uncorrected transposition" (see Spitzer, "Über den Bauplan des normalen und missbilderen Herzens," *Virch. Arch.* Bd. CCXLIII, S. 174 u. 191, 1923) as in the normal heart (see Quain's *Anatomy*, "The Heart," vol. IV, pt. 3, p. 100, 1929) the posterior inter-ventricular artery may be a branch of the left coronary artery, there seems to be no record in these cases of the anterior inter-ventricular artery having been observed to be a branch of the right coronary artery. It is apparently also unknown in these cases (and there is no record of the coronary artery origin and distribution in the published cases of "corrected transposition") to find a coronary vessel arising, as in this case, opposite the non-septal cusp of the aorta (see Keith, "Malformations of the heart," *Lancet*, pt. 2, 1909; Symmers, "Accessory coronary arteries," *J. Anat.* vol. XLI, p. 141).

[1] See Griffith, *J. Anat.* vol. XXXVII, p. 251. The factors which govern the change in position of the orifice of the left horn of the sinus vinosus from the position and valvular relations it has as the left superior cava to the position and valvular relations it has when it forms the collecting stem of the cardiac veins have still to be determined. The dissociation of the anterior inter-ventricular vein from the coronary sinus has been noted in *situs inversus* of the atria with normal ventricles; see Yater, *Amer. J. Dis. of Children*, vol. XXXVIII, p. 118.

[2] In a further communication the position of the a.-v. node will be described.

The pars membranacea septi is longer in its antero-posterior extent than usual for it extends backwards between the a.-v. orifices along the upper edge of the posterior part of the ventricular septum, as far as their hinder parts (fig. 3 A). In relation to the arterial cusps its fore part is situated below the left cusp of the pulmonary artery, which position represents a reversal of its normal position below the right cusp of the posterior vessel—the aorta—in the normal heart (fig. 3); and, further, its atrio-ventricular part intervenes not between the right atrium and the left ventricle, as is normal, but between the left atrium and the ventricle of the right side. I have understood from this that the posterior part of the ventricular septum met and fused with the septum intermedium not close to the right atrio-ventricular orifice as in the normal heart (fig. 5 A) but close to the left orifice (fig. 5 B), and that it lay, in reference to the atrial canal, to the left of its usual position[1].

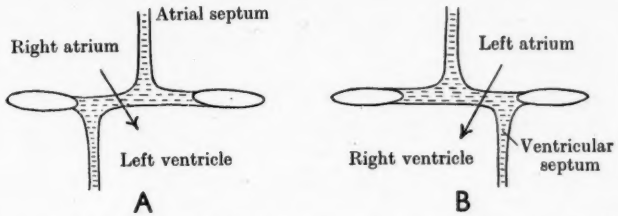


Fig. 5. Diagram of the formation of the atrio-ventricular septum in (A) the normal heart, and (B) a case of "corrected transposition." The arrow passes through the septum, which is considered to be a part of the septum intermedium.

The internal conformation of the ventricles of this heart is peculiar. In the ventricle of the left side (fig. 6) the trabeculation has the coarse form and the vertical arrangement which are normally characteristic of the right side, and there is also present the profuse apical trabeculation which is usually found in the right ventricle. There is a well-developed crista supraventricularis above and a moderator band formation below, so that the subdivision of the ventricle which is normally typical of the right ventricle is here present in the ventricle of the left side. The crista supraventricularis (figs. 6 and 3) is a broad flat muscular bundle on the roof of the ventricle, being much less elevated there than is often to be observed in normal hearts; but when followed downwards on to the septum (fig. 6 B) it is continued into a very prominent muscle mass which intervenes between the front and back parts of the ventricular cavity. The moderator band formation, which is of large size and which is continuous below with the apical trabeculae, is continued from the

[1] I would point out here—a full account will be given in a later paper—that to reach the ventricular septum the course of the stem of the a.-v. bundle through the fibrous tissue at the base of the ventricles must be much longer in the "transposed" than in the normal heart (fig. 5); and, after microscopic examination of the parts, I believe that the fibrosis which has occurred in the main stem—the right limb of the bundle being normal in its appearances—was the cause of the heart block.

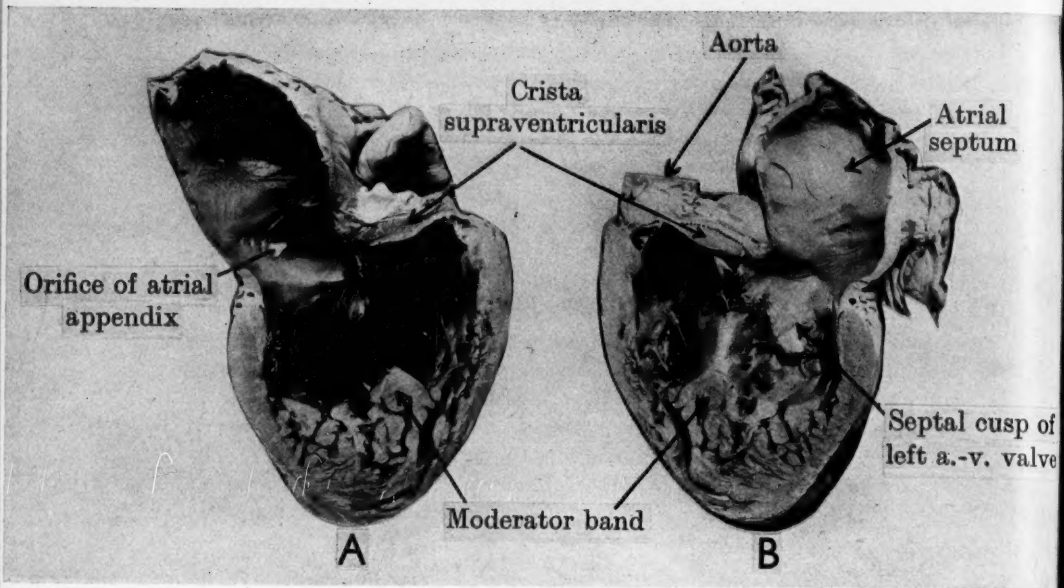


Fig. 6. The interior of the left chambers of the heart. A, the lateral parts, and B, the septal parts.

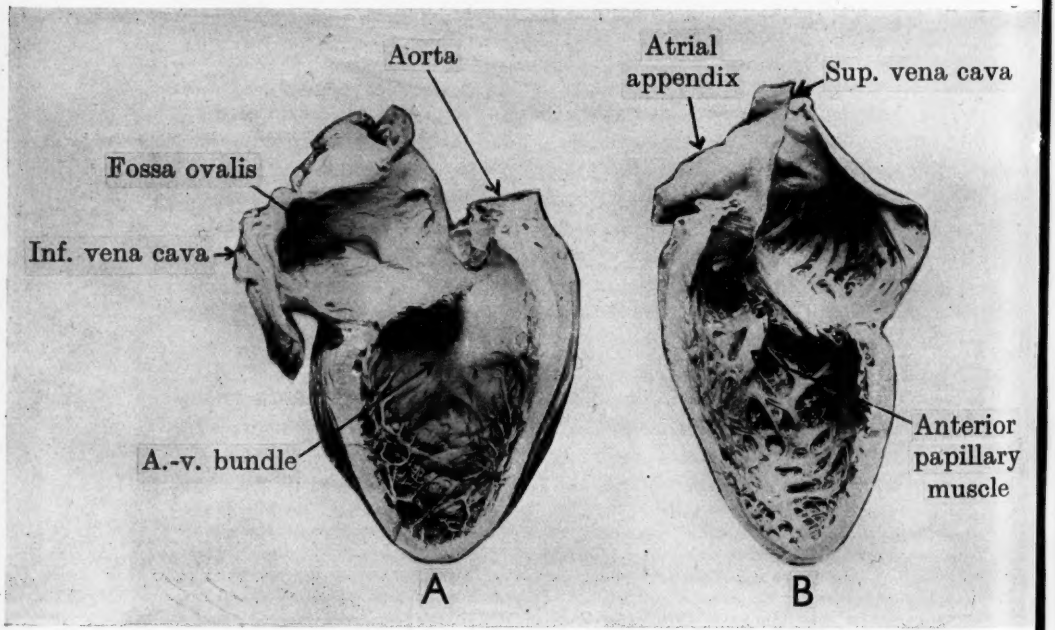


Fig. 7. The interior of the right chambers of the heart. A, the septal parts, and B, the lateral parts.

lower end of this mass to the lateral wall of the ventricle; the two parallel parts of which it has been said to consist (Spitzer) could not be defined. The anterior papillary muscle arises from its posterior aspect close to its lateral end. The infundibular (anterior) part of the ventricle is coarsely trabeculated on all its walls up to the bases of the arterial cusps, as is sometimes to be found in the infundibulum of the right ventricle of the normal heart; but the downward extension of this cavity below the moderator band[1] is represented only by a broken-up slit-like space among the trabeculae.

The left a.-v. valve (figs. 3 A and 6) consists of three cusps and these are so placed that the valve more closely represents a reversed tricuspid valve[2] than a division of the posterior cusp of a normal mitral valve into the two parts of which it is formed. The anterior cusp is the largest and strongest. It is incised near its medial end, indicating a partial non-union of the two anterior elements (see references in footnote 2 below) of which it is formed. It receives entirely on its ventricular surface the subdivisions of six large chordae tendineae from the anterior papillary muscle and at its edges smaller chordae from the posterior papillary muscle and from the septum; and it is distinguished from an aortic mitral cusp by the fact that some of these chordae reach nearly to its base before they are inserted into its substance. The septal papillary muscles, the chordae tendineae of which are attached to its medial part, are two in number; and their bases are attached to the septum along the anterior edge of the septal extension of the crista supraventricularis, as is usual in the normal right ventricle[3]. The front part of the base of the septal cusp of the valve crosses the fore part of the septum membranaceum, dividing it, as the septal cusp of the tricuspid usually does, into atrio-ventricular and ventricular parts. The chordae tendineae of this cusp arise directly from the

[1] The author believes this part of the right ventricle to be a specific part of the chamber, formed, as it were, by a process of excavation from above downwards in the anterior wall. It is very variable in its size, and when it is absent—as is sometimes to be observed in the human heart and as is so marked a feature in birds—the moderator band formation is incorporated in, and forms part of, the anterior wall.

[2] The tricuspid condition of the left a.-v. valve which has been described to occur in specimens of "corrected transposition" of the arterial stems, such as this case is, is not—at least as it is figured by Vierordt (Nothnagel's *System*, 1898) and Abbot (Osler and McCrae, *System of Medicine*, vol. IV, 1908)—a reversal of the normal right tricuspid valve as is present in this specimen and shown in fig. 3 A, but might be explained as a division of the posterior cusp of a normal mitral valve. It is true that the observations of Mall ("The development of the heart," *Amer. J. Anat.* vol. XIII, 1912) and Shiro Sato ("Über die Entwickelung der Atrioventricularklappen," *Anat. Hefte*, Bd. L, 1914) on the developmental history of the a.-v. valves detract from the significance of the a.-v. valve form in determining the nature of the ventricle, but the reversal of both sides is here so definite that I believe I am justified in using it as is done later in the discussion.

[3] Spitzer ("Über den Bauplan des normalen und missbildeten Herzens," *Virch. Arch.* Bd. CCXLIII, 1923) distinguishes in the right ventricle a region—the conus of the right aorta (fig. 3 B)—between the anterior cusp of the tricuspid valve and the crista supraventricularis, and in discussing the morphology of the crista holds that it intervenes not between an ingoing and an outgoing part but between two outgoing parts of the ventricle, the pulmonary orifice in front and the right aortic region behind. He does not consider the position of the origin of the septal papillary muscles, which, as it is described here, would not readily form part of his interpretation.

septum and from the more medial of the two small posterior papillary muscles. The papillary muscles of this ventricle have thus the form, size, and position which are characteristic of the muscles of the right ventricle.

In the ventricle of the right side (fig. 7) the trabeculation is fine, like that which is usual in the left ventricle, but the upper half of the septum is smooth; and this smooth area is bounded above by a limbus marginalis (His) as is usually found on the left ventricle. There is no crista supraventricularis and no moderator band formation. It is possible to identify on the septum a formation and a distribution of the a.-v. bundle limb which are normal in the left ventricle; that is, it is possible to identify (and the identification was confirmed by histological examination) a broad flat band of a.-v. tissue on the upper part of the septum and to follow it downwards to its division into anterior and posterior branches and to trace these branches to their distribution among the apical trabeculae[1]. There are two cusps in the atrio-ventricular valve, which are arranged as is shown in fig. 3. The cusp which intervenes between the a.-v. and pulmonary orifices is much longer and thicker than the posterior cusp, and shows no tendency to the subdivision which is shown on the posterior cusp; its basal attachment is wholly above the membraneous septum. The chordae tendineae of the cusps arise from large anterior and posterior papillary muscles, which in their size, position, and form resemble those which are normally present in the left ventricle (fig. 7).

As measured on the anterior walls near the base of the ventricles, the wall of the right ventricle is 0·35 inch and that of the left ventricle 0·55 inch in thickness.

DISCUSSION

This heart is an example of the very rare condition which was named "corrected transposition" by Rokitansky[2], and the description of it in his terms would be that the relation of the arterial vessels to one another had been altered by an abnormal deviation of the aortico-pulmonary septum so that the trunks had been transposed, and that the transposition had been "corrected" by a reverse deviation of the ventricular septum from its normal position, in that it now surrounds the posterior vessel on its left instead of its right wall (fig. 3 A), so that the vessels arise from their proper ventricles. It has long been recognised that though Rokitansky's general explanation of the transposition of the arterial stems is a masterly elucidation of an obscure subject, this description of "corrected transposition" is incomplete, and several modifications of it and additions to it have been proposed; but as examples

[1] Cp. fig. 56, p. 83, Quain's *Anatomy*, vol. IV, pt. 3. This reversal of the form of the a.-v. limbs has already been noted in a case of "corrected transposition" by Shiro Sato ("Über die Entwickelung der Atrioventricularklappen," *Anat. Hefte*, 151 Hefte, Bd. L, Hefte 2, S. 244, 1914). A similar case of transposition of the a.-v. limbs was described by Mönckeberg (*Verh. d. Deutsch. path. Gesellschaft*, Marburg, 1913) in a complicated malformation of the ventricular septum. I have not yet been able to identify the left limb, that is, it is not present in a recognisable form in the moderator band.

[2] Rokitansky, *Die Defekte der Scheidewände des Herzens*, Wien, 1875.

of the condition are uncommon[1], and as in the descriptions of some of the earlier cases references to the important features have been omitted, some of the newer matter is very largely theoretical. In the six examples collected by Abbot[2] the aorta and pulmonary artery are reversed in their relation to one another (as in the case described here, fig. 3 A) and they arise from their proper ventricles; in all of them there is a defect of the inter-ventricular septum at its base (there is no defect in the present specimen); and in all of them the a.-v. valve formations are transposed as in this case (but see p. 535, footnote 2), the mitral formation being in the ventricle of the right side and the tricuspid formation in the ventricle of the left side. It is obvious that the reversal of the a.-v. cusp formations, which is a common character of all the recorded examples, cannot be accounted for by a simple deviation of the septum.

Lochte[2], having described his specimens, especially the second, in great detail, put forward as the explanation of the condition the occurrence of a left to right twisting of the left ventricle round the right ventricle, instead of the normal right to left twisting of the right round the left ventricle, with a corresponding deviation of the ventricular septum which brings about the transposition of the a.-v. valves; and the anomalous position of the arteries he considers to be due to an impeded torsion of the bulbus. But though this condition of ventricular torsion may occur[3], its interpretation presents great

[1] Spitzer (1923) has made the following analysis of the 16 cases which are described in the literature as examples: (1) and (2) Two cases by Rokitansky in infants (four months and eleven months old). (3) A case of Rokitansky's cited as such by Vierordt; but it belongs to the opposite type of "uncorrected transposition." (4) A case reported by Gamage, *New England Jour. of Med. and Surg.* vol. IV, 1818. (5) Rauchfuss, in Gerhardt's *Handb. d. Kinderkrankheiten*, Bd. IV. Abt. 1, 1878. (6) Tönnies, "Über eine seltene Missbildung des Herzens," Inaug. Diss. Göttingen, 1884. (7) Mann, *Beiträge z. path. Anat.* Bd. XVI, 1889. (8) Grunmach, *Berl. klin. Wochenschr.* 1890. (9) Graanboom, *Zeitsch. f. klin. Med.* Bd. XVIII, 1891; this is really an example of "uncorrected transposition" with *situs inversus* of the atria. (10) and (11) Two cases by Lochte, *Beiträge z. path. Anat.* Bd. XVI, 1894 and Bd. XXIV, 1898. (12) and (13) Two cases by Geipel, *Arch. für Kinderheilk.* Bd. XXXV, 1903. (14) and (15) Two cases are mentioned, without description, by Keith, *Lancet*, vol. LXXXVII, pt. 2, 1909. (16) Shiro Sato, *Anat. Hefte*, Bd. L, 1914.

In addition to these cases there are two mentioned by Abbot which occurred in Thérémin's series (*Études sur les affections congénitales du cœur*, Paris, 1895) and there should also be included two cases described by Young and Robinson (*Med. Chron.* Manchester, Nov. 1907). The six cases described by Abbot are the two cases of Thérémin, the two of Rokitansky, and those of Rauchfuss and Tönnies

[2] See footnote above.

[3] I have been fortunate enough to see this condition. It occurred in a human embryo of 5·5 mm. C.R. length belonging to Prof. C. J. Patten, and I am much indebted to him for the permission he gave me to model the heart and to include a reference to it here. The embryo showed a very great dorsal concavity and a considerable straightening of the head region; and these abnormalities had prevented, I believe, the normal expansion of the dorsal wall of the pericardium. The ventricular loop lies almost in a sagittal plane on the right side of the heart, the descending limb of the loop being in front and the ascending limb behind and resting on the dorsal wall of the pericardium. At its upper end the ascending limb turns downwards (caudalwards) and forms a loop with the convexity towards the head and then passes backwards to pierce the dorsal wall of the pericardium at about one-third its proper distance from the area of the septum transversum from which the sinus venosus emerges. This looped part lies behind and to the right of the atrial canal, which has been displaced to the left. The atrial part of the heart is small in size, especially the right part which has been unable to expand behind the ascending limb of the ventricular loop.

difficulties for it must be accompanied by irregularities in the hinder parts of the heart which are not referred to by Lochte; and it is obvious that it would require considerable readjustments of development to bring the ventricular bulbus region, which during the early stages lies on the posterior part of the heart, to occupy the most ventral position of the adult heart.

The only other explanation[1] that there is in this condition a *situs inversus* of the ventricular loop, the descending limb of the loop being on the right side and forming what is here the right ventricle and the ascending limb on the left and forming the ventricle of the left side, is strongly supported by the arrangements of the ventricles of this specimen; and as the primary anomaly of this heart it would be sufficient, I believe, to account for the reversal of the a.-v. valve formations, the reversal of the internal conformation of the ventricles, the incidence of the atrio-ventricular part of the pars membranacea septi, the reversal of the form of the limbs of the a.-v. bundle, and the reversal of coronary artery fields. This explanation postulates an independence of the ventricular loop from the other parts of the cardiac tube during the early stages of development. Such an independence is easily conceived, and that it does occur seems to be proved by those cases of total transposition of the viscera, including the atria of the heart, in which, however, the ventricles are not transposed[2]; and the recognition of the ventricles by their internal features, as has been claimed in this account, is the more certainly correct if it be noted that in no case of complete *situs inversus* of the viscera (including the ventricles of the heart) has there been any doubt of the inversion of the ventricles on account of anomalies in the structure of these chambers.

The primary anomaly of this heart is then, I believe, an inversion of the ventricular loop, so that what is here the ventricle of the right side is the descending limb of the loop and morphologically the left ventricle, and what is the ventricle of the left side is the ascending limb and morphologically the right ventricle. This explanation would account for the structural features of the specimen and also for the left-sided position of the ventricular septum; and further it would produce a rotation of the ventricular septum and of the proximal bulbar septum in a direction the reverse of normal, that is in a left-winding in place of a right-winding spiral (fig. 8), and the infundibulum, formed from the anterior part of the proximal bulbus as usual[3], will be included in the ventricle of the left side. Now in all the cases of "corrected

[1] This explanation has been suggested by Robertson ("The comparative anatomy of the bulbus cordis," *J. Path.* vol. XXVIII, 1913–14), Shiro Sato, and Spitzer, and is referred to, with modifications, by Bremer ("An interpretation of the development of the heart," *Amer. J. Anat.* vol. XLII, 1928).

[2] Such cases have been reported by Keith and MacDonnell ("Case of transposition of the viscera showing a potentially bicameral heart," *Proc. Roy. Soc. Med.* vol. XIV, 1921) and Yater ("Congenital heart block," *Amer. J. Dis. of Children*, vol. XXXVIII, 1929); in the latter paper the literature is reviewed.

[3] In *situs inversus* of the ventricular loop the proper anterior surface of the ascending limb and of the bulbus will remain on the anterior surface, just as the anterior surface of the inverted stomach is the proper anterior surface.

transposition" in which the facts have been recorded the aorta forms a normal left aortic arch, and at its termination the pulmonary artery occupies its normal position behind the aorta. I wish therefore to suggest that in these cases the

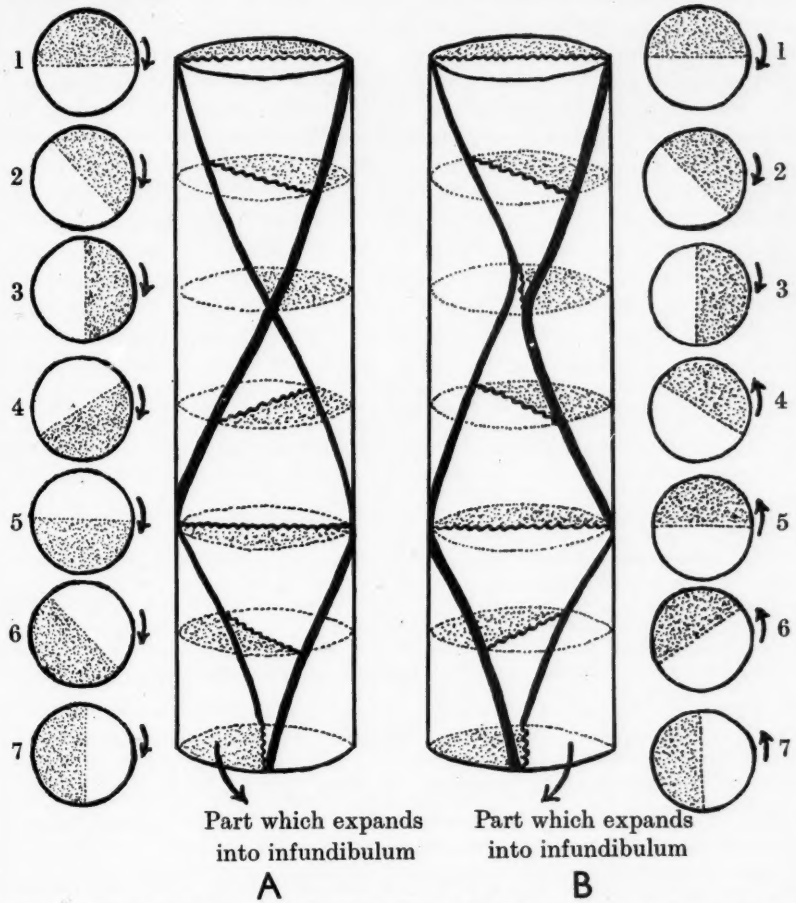


Fig. 8. Diagrams to illustrate the course of the ventriculo-bulbar and aortico-pulmonary septa in A, the normal heart, and B, a heart with transposed ventricles.

aortico-pulmonary and distal bulbar septa have rotated normally, there being no inversion of these parts, and that, therefore, the anterior arterial stem is, as normally, continued into the right orifice at the base of the heart and the posterior stem into the left orifice (fig. 8 A, 1–3 and B, 1–3)[1]. Below this

[1] See the diagrams by Keith ("Malformations of the heart," *Lancet*, 1909, pt. 2, and "The fate of the bulbus cordis," *Lancet*, 1924, pt. 2).

position, however, the rotation of the ventricular and proximal bulbar septum being the reverse of normal in the transposed heart, the posterior arterial stem will continue its course from the left orifice in the direction the reverse of normal. It will pass again, therefore, to the posterior aspect of the anterior vessel (fig. 8 B, 4–7), instead of to its anterior aspect, but it will be continued, as is normal, into the ventricle of the right side; and the anterior arterial stem, from its position on the right at the base of the heart, will be continued into the ventricle of the left side, which as already indicated will include the infundibulum. I would suggest, therefore, that the transposition of the arterial stems is the direct result of the transposition of the ventricles combined with a normal rotation of the aortico-pulmonary septum[1]; that is, that the only anomalous condition which is present in "corrected transposition" is the *situs inversus* of the ventricular loop, and that the straight course of the aorta and pulmonary artery relative to one another is the simple straightening out of two opposite spiral curves[2]. In the specimen which is described here these opposite rotations have occurred perfectly and the septation of the heart is complete; in this respect it is a unique heart.

[1] I have not thought it necessary to enter into the explanation advanced by Spitzer. This is founded on two premises: (1) that transposition of the arterial stems not being a condition of any stage of normal development cannot be due to purely ontogenetic factors; and (2) that the mammalian heart is in direct evolutionary series with the existing reptilian heart. On these premises Spitzer has founded the conclusion that "uncorrected transposition" of the stems is due to the gradual opening up of the right aorta of the reptilian heart (see fig. 3 B), an opening of the conus region alone producing a "riding aorta" with a basal defect of the ventricular septum, and a total suppression of the left aorta producing a condition in which both pulmonary artery and right aorta will arise from the right ventricle. He also postulates, however, a mal-rotation of the bulbus which brings the aorta in front of the pulmonary artery; and, in an extremely suggestive section on the constitution of the ventricular septum, holds that the anterior part of the ventricular septum (fig. 3 B, 1–2) in the more advanced abnormalities is really the very greatly developed crista supraventricularis, and that what is the crista supraventricularis is the true but greatly regressed anterior part of the septum.

The premises of these descriptions do not seem to me to be sound, and the descriptions themselves, I think, require to be re-examined, but when they are applied to "corrected transposition," in which condition Spitzer believes they occur with a *situs inversus* of the ventricular loop, it is certain they do not agree with the facts; for as is shown in figs. 3 A and 3 B the "transposed" heart is the mirror image of the normal heart and not of a heart with a right aorta, the only difference of the image being the stem of origin of the coronary arteries. Further, if Spitzer's account were correct, and if what is named here the crista supraventricularis (fig. 3 A) were the proper anterior part of the septum, then the crista supraventricularis (what is named here the anterior part of the septum (fig. 3 A, 1–2)) is in an unreversed position; and this would render it impossible to name the arterial orifices at all.

[2] It is this straight course of the vessels which has given rise to the very common description that there has been an absence of rotation.

ANATOMY OF THE REGION CONCERNED IN FEMORAL HERNIA IN INDIANS (IN BENGAL)

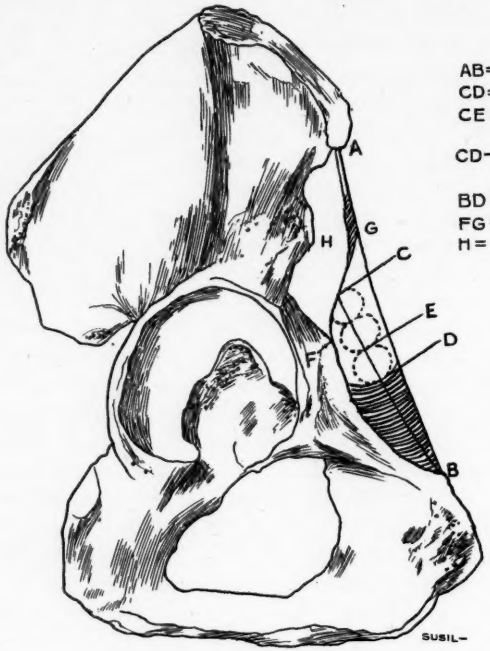
By N. PAN

Professor of Anatomy, Medical College, Calcutta

In July, 1929, Lt.-Col. Sir Frank Connor, I.M.S., Professor of Surgery, Medical College and Surgeon to the Medical College Hospitals, drew my attention to the fact that femoral hernia was extremely rare among Indians and asked me to make some observations on the subjects brought to the dissecting hall with a view to explaining this fact on anatomical considerations. The incidence of the disease is so rare that in the course of fifteen years during which he has been connected with the Medical College Hospitals Sir Frank Connor has operated once only for the radical cure of femoral hernia. During the last thirteen years nearly 2000 subjects have been dissected in the Anatomy Department of this College and I have not met with a single instance of femoral hernia or even of a preformed sac in the crural canal. This is of greater significance than the hospital statistics. Accepting the view that femoral hernia is more common in females, and knowing that Indian females would never come to a hospital for an operation of femoral hernia unless it is strangulated, one would naturally expect to meet with cases of femoral hernia among the subjects brought to the dissecting hall if the disease were as prevalent in India as it is in Europe and in America. Hospital statistics and dissecting hall records both confirm the fact that femoral hernia is extremely rare here.

In most of the text-books on surgery(1) the factors predisposing to the occurrence of femoral hernia are said to be (*a*) a larger size of the crural ring associated with (*b*) a smaller and more poorly developed Gimbernat's ligament. Hence investigations were made with a view to ascertaining the size of the crural ring and the condition of Gimbernat's ligament. The rare incidence of femoral hernia would be explained if the ring be smaller and Gimbernat's ligament larger and better developed in Indians than in other races. With this object in view careful dissections were made of 58 subjects, of which 35 were males and 23 females. As the observations were made on both sides of the body 116 parts concerned in femoral hernia were actually dissected. On comparing the resulting figures on the two sides of the body it was found that the differences between the measurements on the left and right sides were so small as to be negligible. For this reason the observations on the right side of the body only have been incorporated in the annexed tables. In both male and female series most of the subjects were adults, their ages ranging from 30 to 50. The part that has been carefully dissected and from which measure-

ments have been taken is the irregular interval between Poupart's ligament in front and the iliac and pubic parts of the hip bone lying immediately behind the ligament (fig.). This interval or space has been conveniently named the "Pelvo-crural interval" by Panton in his article published in the *Journal of Anatomy* in January, 1923. The ilio-pectineal ligament stretches from the ilio-pectineal eminence behind to Poupart's ligament in front, passing obliquely



forwards and lateralwards making an acute angle with Poupart's ligament medially. The average measurement of this angle is 30°. This oblique ligamentous band subdivides the "Pelvo-crural interval" into two compartments, the outer, the lacuna musculosa, lodging the ilio-psoas muscle and the inner, the lacuna vasculosa, which transmits the crural sheath with its three compartments. The following measurements have been recorded:

I. LENGTH OF POUPART'S LIGAMENT

The distance between the anterior superior iliac spine and the pubic spine has been noted as representing the length of Poupart's ligament although the ligament in the recent state is not straight, and owing to its convexity towards the thigh is slightly longer than that represented by this measurement. Table A represents the female measurements and Table B those of the

males. It will be observed that in the females the length varies from 96 mm. to 118 mm. with an average of 108 mm., whereas in males it varies from 97 mm. to 128 mm. with an average of 112 mm. Thus Poupart's ligament is on an average slightly longer (by 4 mm.) in males.

II. BREADTH OF THE ILIO-PSOAS MUSCLE

This has been ascertained by measuring the distance between the anterior superior iliac spine and the ilio-pectineal eminence at the medial border of

Table A. *Female cases* (*right side*)

	1	2	3	4	5	6	7
Serial no.	Length of Poupart's ligament	Breadth of ilio-psoas	Distance between medial border of ilio-psoas and pubic spine	Transverse diameter lacuna vasculosa from lateral side of femoral vessels to Gimbernat's ligament	Transverse diameter femoral vessels	Transverse diameter crural ring	Transverse diameter Gimbernat's ligament
1	103	64	41	28	19	9	34
2	111	65	53	29	17	12	30
3	106	62	47	28·5	16	12·5	34
4	100	64	43	24	15	9	30
5	109	66	50	24	14	10	28
6	106	60	50	28	15	13	34
7	97	64	48	32	20	12	30
8	108	67	49	35	20	15	32
9	118	66	59	28	17	11	36
10	118	67	60	35	25	10	32
11	110	62	53	24	19	5	33
12	102	60	50	23	15	8	26
13	110	64	50	25	15	10	29
14	110	62	60	26	20	6	32
15	113	70	48	30	20	10	38
16	115	65	57	31	20	11	40
17	106	63	48	33	20	13	26
18	96	51	50	26	15	11	27
19	112	70	48	28	16	12	33
20	99	55	52	28	18	10	30
21	115	65	57	28	18	10	39
22	110	63	55	24	18	6	35
23	101	60	46	29	18	11	29
Totals ...	2475	1455	1174	646·5	410	236·5	737
Average ...	107·6	63·2	51	28	17·8	10·2	32
Female ...	108	63	51	28	18	10·2	32

N.B. All measurements are in millimetres.

the muscular mass. The average width in the female series is 63 mm., whereas in the male series it is 66 mm. Thus the breadth of the ilio-psoas is greater in the male by 3 mm. One would expect that the difference in the two sexes would be greater owing to the greater muscular development in the male. But the comparatively small difference is probably due to the fact that the female subjects received at the dissecting hall mostly belong to the labouring classes in which the women participate in manual work with men, and hence their muscular development is fairly good in comparison with that of females who occupy higher social positions and lead a more sedentary existence.

III. BREADTH OF LACUNA VASCULOSA

This has been measured from the lateral side of the femoral artery to the centre of the concavity of the free margin of Gimbernat's ligament. This measurement does not correspond with the measurement taken from the medial

Table B. *Male series* (*right side*)

Serial no.	1 Length of Poupart's ligament	2 Breadth of ilio-psoas	3 Distance between medial border of ilio-psoas and pubic spine	4 Transverse diameter lacuna vasculosa	5 Transverse diameter femoral vessels	6 Transverse diameter crural ring	7 Transverse diameter Gimbernat's ligament
1	109	70	48	26	13	13	30
2	105	65	45	26	16	10	26
3	121	76	53	35	22	13	34
4	116	72	51	26	15	11	30
5	105	65	50	32	17	15	28
6	113	62	57	34	21	13	29
7	112	73	56	30	15	15	29
8	97	57	46	28	17	11	33
9	110	70	50	30	15	15	30
10	114	69	50	29	14	15	30
11	106	59	52	25	15	10	36
12	128	72	63	33	19	14	33
13	119	76	53	25	18	7	31
14	115	64	60	31	22	9	37
15	121	70	65	35	25	10	34
16	110	65	60	29	20	9	33
17	110	70	54	28	17	11	35
18	114	70	59	29	15	14	33
19	108	60	53	28	18	10	26
20	115	68	56	26	14	12	35
21	114	65	56	30	20	10	30
22	105	64	54	33	23	10	30
23	106	65	49	28	18	10	31
24	106	60	51	25	15	10	30
25	110	65	52	28	20	8	28
26	106	59	52	25	15	10	36
27	104	57	52	25	16	9	30
28	105	57	53	34	24	10	25
29	101	55	52	30	18	12	28
30	102	55	52	26	16	10	36
31	114	66	54	35	23	12	27
32	116	68	52	29	20	9	35
33	110	67	50	29	20	9	32
34	128	72	60	32	20	12	38
35	128	75	58	30	20	10	35
Totals ...	3903	2303	1878	1024	636	388	1103
Average ...	111·514	65·8	53·657	29·2	18·1	11	31·514
Female ...	112	66	54	29	18	11	32

N.B. All measurements are in millimetres.

border of the ilio-psoas to the same point in the Gimbernat's ligament; for the femoral vessels overlap the medial side of the ilio-psoas to the extent of about 8 mm. on an average (9 mm. in females and 7 mm. in males) as will be evident from Table D. In females the transverse measurement of the

lacuna vasculosa is, on an average, 28 mm., whereas in males it is 29 mm. This difference is negligible, and it may be said that this measurement is practically identical in the two sexes.

IV. TRANSVERSE DIAMETER OF THE FEMORAL VESSELS

In the dissecting-hall subjects the femoral arteries retain their shape being injected with colouring material, whereas the femoral veins lie collapsed and flattened. The actual measurements of these two vessels in this condition has been taken and it is found that both in males and females the average diameter is identical, viz. 18 mm. The collapsed and flattened condition of the femoral vein is not a criterion of its condition in the living subject, the transverse diameter of the vein being relatively greater in the cadaver. To eliminate this error and thereby arrive at the accurate transverse measurement of the femoral vessels, the femoral vein was moderately distended with fluid in some subjects. By comparing the measurements in the collapsed and distended conditions it was found that the former measurement exceeded the latter by 2 mm. Consequently by reducing the average measurement (18 mm.) by 2 mm. the actual measurement of the vessels in the living subject (16 mm.) is arrived at with greater accuracy. This average transverse measurement of the femoral vessels corresponds to that which Panton has accepted as the most likely average (2).

V. TRANSVERSE DIAMETER OF THE CRURAL RING

Table C

	Transv. diameter lacuna vasculosa		Transv. diameter femoral vessels		Crural ring
Female ...	28 mm.	–	16 mm.	=	12 mm.
Male ...	29 mm.	–	16 mm.	=	13 mm.

By deducting the transverse diameter of the femoral vessels from that of the lacuna vasculosa the transverse diameter of the crural ring was calculated to be 12 mm. in females and 13 mm. in males. The actual measurements of the crural ring were also noted in both series and were found to be 10·2 mm. in females and 11 mm. in males. However, it has already been pointed out that the crural ring had been encroached upon to the extent of 2 mm. by the collapsed femoral vein. Consequently by adding 2 mm. to these actual measurements of the crural ring the same figures are obtained as those arrived at by the indirect method, viz. 12 mm. for females and 13 mm. for males. Hence the direct measurement of the crural ring, the accuracy of which is questionable, is corroborated in these cases by the indirect and more accurate method as shown in Table C. The antero-posterior diameter of the crural ring has also been measured in all the subjects examined. Although the measurement cannot be regarded as absolutely reliable on account of the flaccid condition of Poupart's ligament the average in both males and females is the same, viz. 9 mm.

VI. TRANSVERSE MEASUREMENT OF GIMBERNAT'S LIGAMENT

This has been taken from the apex of the pubic spine to the centre of the base or free margin of the ligament. This measurement is, on an average, 32 mm. in both series. Panton found 2 cm. to be the average transverse measurement of this ligament in both sexes. According to Gray (3) the transverse diameter of this ligament is 2 cm., and according to Buchanan (4) 2·5 cm. This ligament is therefore much broader in the subjects examined here. Not only is the extent of attachment of this ligament greater but it is always thick and well developed. In no single instance has a poorly-developed Gimbernat's ligament been noted. The average proportional length of this ligament to Poupart's ligament is 1 : $3\frac{1}{2}$, whereas in Panton's series it was 1 : 6. Thus Gimbernat's ligament is much larger absolutely and also proportionately to Poupart's ligament.

VII. MEASUREMENT FROM MEDIAL BORDER OF ILIO-PSOAS TO THE PUBIC SPINE

This measurement has been taken in order to ascertain the extent to which the medial border of the ilio-psoas is overlapped by the femoral vessels. The average measurement in females is 51 mm. and in males 54 mm.

Table D

Lacuna vasculosa from lateral side of femoral vessels to Gimbernat's ligament		Gimbernat's ligament (transverse diameter)		From medial border of ilio-psoas to pubic spine		Overlapping of ilio-psoas by femoral vessels
In females 28 mm.	+	32 mm. = 60 mm.	−	51 mm.	=	9 mm.
In males 29 mm.	+	32 mm. = 61 mm.	−	54 mm.	=	7 mm.

Thus there is an overlapping of the medial part of the ilio-psoas to the extent of 9 mm. in females and 7 mm. in males. By referring to Tables A and B it will be observed that in some cases the femoral vessels almost completely overlie the ilio-psoas. This explains why the ilio-pectineal ligament is not a straight antero-posterior band but an oblique one, the obliquity being so marked that the anterior end of this ligament makes an angle of 30° with Poupart's ligament medially.

CONCLUSIONS

The extreme rarity of femoral hernia in Indians is due to the following reasons:

1. The average size of the crural ring is 12–13 mm. which may be regarded as normal, as 1·25 cm. is the average measurement noted by Gray and Cunningham (*Practical Anatomy*).

2. Gimbernat's ligament is absolutely and relatively larger in size, being 3 cm. in transverse diameter. The larger size of this ligament together with its constant thickness and potent development ensure strength of the part. Thus the two factors which predispose to the occurrence of femoral hernia are both absent in Indians.

The exciting causes are said to be overstretching and consequent weakening of the abdominal muscles during pregnancy, straining at stools in constipated subjects and in those suffering from chronic dysentery, etc. The peculiar squatting position assumed by the Indians in defoecation effectively closes the crural ring and thus excludes the latter factor from the etiology of femoral hernia. Moreover, constipation is not so frequent among the Hindu population of the district on account of the bulky carbohydrate food taken which, leaving much residue after absorption, stimulates peristalsis mechanically and causes easy evacuation. Many observers have noticed the presence of a preformed sac in the crural canal. But its absence in all the cases observed removes this etiological factor in femoral hernia.

My thanks are due to the colleagues of my department, and specially to Dr Bepin Behari Basak, for their help and co-operation in carrying out these observations.

REFERENCES

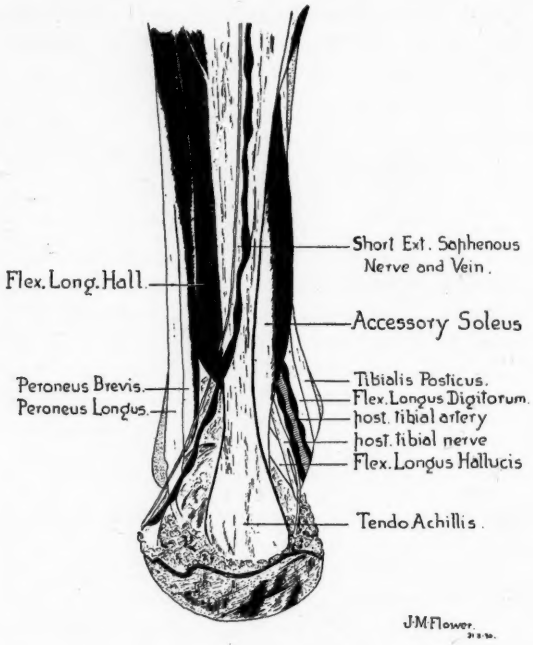
(1) Rose and Carless's *Manual of Surgery*; Gask and Wilson's *Surgery*; Thomson and Miles.
(2) Panton, J. Allison (1923). "Factors bearing upon the etiology of femoral hernia." *J. Anat.* vol. LVII, p. 106.
(3) Gray's *Anatomy*.
(4) Buchanan's *Manual of Anatomy*.

NOTE ON AN ACCESSORY SOLEUS MUSCLE

By J. M. FLOWER

Medical Student, King's College, London

In the course of prosection of the back of the left leg of a male subject, an anomalous muscle was seen springing by a tendinous origin from the anterior or deep aspect of the tendon of the soleus. Covered at first by the tendo Achillis, the tendon broadened out distally and acquired a fleshy belly which was inserted on the os calcis by a separate tendon internal to the insertion of the tendo Achillis (fig.). The condition was unilateral.



From the point of view of comparative anatomy the soleus is a variable muscle, present in some animals and absent in others.

Le Double records cases of a supernumerary soleus in man, situated in front of the normal soleus, with an origin similar to that of the soleus, and inserted on the os calcis by a separate tendon.

He refers to four dissections of "a musculo-tendinous cord" arising from the deep aspect of the soleus and inserted on the os calcis internal to the insertion of the tendo Achillis. The plantaris was present in two of the cases and absent in one; its presence or absence in the fourth was not recorded.

The accessory muscle under consideration appears to be intermediate between the delaminated muscle type and the tendinous cord type.

Testut (referred to by Le Double) regards the accessory soleus muscle as a variety of plantaris. Le Double refutes this view, as the accessory muscle may be present when there is also a normal plantaris. It arises with the soleus, and not from the femur where the plantaris arises. The muscle springs from the anterior or deep surface of soleus, whereas the plantaris tendon passes between the soleus deeply and the gastrocnemius superficially.

The accessory muscle is probably to be regarded as a detached portion of the normal soleus.

REFERENCE

LE DOUBLE. *Traité des variations du système musculaire de l'Homme*, t. II. Paris, 1897.

RECENT APPOINTMENT

UNIVERSITY OF EDINBURGH CHAIR OF ANATOMY

At the end of the present academic year Prof. Arthur Robinson resigns from the Chair of Anatomy in the University of Edinburgh which he has occupied for 22 years. In 1909 he was invited from the Chair of Anatomy in Birmingham to occupy that of his old University on the death of Prof. D. J. Cunningham—the leading British anatomist of his time. Prof. Robinson has devoted nearly half a century to the pursuit of his chosen subject; readers of this *Journal* are familiar with the many contributions he has made to its pages—representing embryological researches distinguished by exactness of technique and reliability of statement.

Prof. James C. Brash has been appointed to succeed him and will give up the Chair of Anatomy in Birmingham to take over duties in Edinburgh at the close of the present summer session. Like Prof. Robinson he is a graduate of Edinburgh University and has, like him, served his apprenticeship in England before being called to occupy the Chair of Anatomy in his old University. After going through courses in Arts (M.A., 1906), Science (B.Sc., 1908) and Medicine (M.B., Ch.B., 1910) in the University of Edinburgh, Prof. Brash proceeded to Heidelberg, returning to take up clinical work, passing on to anatomy first in Edinburgh, then in Leeds. Then came the period of the war (1914–19) when he was with the B.E.F. in France. In 1919 he became assistant to Prof. Peter Thompson in the University of Birmingham. In 1922, on the much regretted demise of Prof. Thompson, Prof. Brash was appointed to succeed him. He speedily established himself in Birmingham as a teacher, researcher and organiser, becoming Dean of the Medical Faculty in 1928. In 1930 he visited the Medical Colleges in the United States of America.

He has carried out many more researches than he has published. A number of minor pre-war contributions stand to his credit. Under Prof. Peter Thompson he applied embryological methods to the explanation of clinical problems; he undertook anthropological investigations, but the work by which he is best known relates to growth of palate, jaws and skull. He returned to the old Hunterian method of vital staining by means of madder, thus bringing to light the extremely complex processes involved in the growth of skull and face. Much of what he has ascertained he has taught his students but has not yet published. We venture to forecast for him a successful occupancy of the Chair which has been held by so many anatomists of the highest rank.

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UNIV. OF MICH.

OBITUARY NOTICE

THE LATE DAVID HEPBURN,

C.M.G., V.D., M.D., C.M. (EDIN.), M.R.C.S. (ENG.), F.R.S.E.

In the death of Emeritus Professor David Hepburn the Anatomical Society of Great Britain and Ireland has lost an old friend, and Cardiff an able anatomist and a valued and much loved citizen. David Hepburn, a true Scot, was born in 1858 at Milnathort, Kinross-shire. Receiving his early education at Brand's School he entered the University of Edinburgh. After a distinguished career as a student, during which time he gained medals and prizes, he graduated M.B., C.M., with Honours, in 1881, being awarded the Beaney Prize as the best student of his year in Anatomy, Surgery and Clinical Surgery. He early attracted the attention of Sir William Turner who, in 1881, appointed him a junior member of his staff; on qualification Hepburn worked for some time with Prof. Spence, and it was on Spence's death that he was appointed to the staff of Sir William Turner. Turner was so struck with his capabilities that, at the first opportunity in 1885, he elected Hepburn to be his Principal Demonstrator of Anatomy, a post held from 1876 to 1882 by Daniel John Cunningham. Hepburn obtained the Diploma of M.R.C.S. (Eng.) in 1884 and the M.D. (Edin.), with a gold medal, in 1891.

Three years later the Court of the University, on the recommendation of Sir W. Turner, increased his status by appointing him Lecturer on Regional Anatomy. This post he retained till his appointment to the Chair of Anatomy at University College, Cardiff, in 1903, vacated by Prof. A. Francis Dixon.

In 1912 Hepburn was appointed a member of the General Medical Council and he remained an active member of that body till his retirement in 1927.

Early in his career in Edinburgh Hepburn became keenly interested and an active member in the volunteer movement in Scotland, joining the 2nd Div. V.M.S.C. as Surgeon Captain in 1886. He was also awarded the "V.D." Volunteer Officers' Decoration in March, 1907. At the outbreak of the War he threw himself, with the energy which was so characteristic of him, into hospital administration in addition to his academic work; as Colonel Hepburn, he was in command of the 3rd Western General Hospital in Cardiff, and the fine work that he did as Commanding Officer was rightly recognised and he was awarded the C.M.G. by His Majesty the King in 1917. He also received acknowledgment of the good work done in Cardiff under his command in an appreciative letter from Mr Lloyd George.

Soon after his appointment to the Chair of Anatomy in Cardiff, Hepburn was elected, in 1903, to the office of Dean of the Faculty of Medicine and served in this position till 1922, when he resigned this post.

The strain of combining his military and academic duties and the work

involved in the establishment of the new Welsh National School of Medicine, in 1921, told on his health; he, nevertheless, consented to continue in the Chair of Anatomy beyond the usual span and retired in 1927 and was awarded the title of Emeritus Professor. Even after his retirement he continued to work and until a few months before his death he was engaged in an important study of the hair of Man and other Primates.

Professor Hepburn had the honour of being one of the original members of the Anatomical Society of Great Britain and Ireland, and was President of that Society from 1916 to 1918.

Early in his career he showed an inclination towards anthropology, and his papers on "The Comparative Anatomy of the Muscles and Nerves of the Superior and Inferior Extremities of the Anthropoid Apes" and on "The Integumentary Grooves on the Palm of the Hand and the Sole of the Foot of Man and the Anthropoid Apes" were, among others, of international repute, Prof. Enrico Gioglioli, of Firenze, speaking of the high esteem in which Hepburn was held in Italy for his comparative anatomical and anthropological work. It is interesting to notice that Prof. Brachet at one time attended Hepburn's courses at Edinburgh, and spoke to his then Chief, Prof. Swaen, of Liege, of how much he had appreciated his teacher. His papers show well his great skill as a draughtsman, many of them being illustrated by beautiful drawings from his own pen.

Though largely interested in anthropology he was by no means a strictly specialised anatomist but, as his many publications show, he possessed a wide range of knowledge of the whole subject; a list of Prof. Hepburn's publications is appended to the end of this tribute to his memory, but one might call especial attention here to those mentioned above and to his paper on "The development of diarthrodial joints in Birds and Mammals," to his section on "The Joints" in Cunningham's *Text-book*, to the paper published in *The Scientific Transactions of The Royal Dublin Society* on "The papillary ridges on the hands and feet of Monkeys and Men," and to his paper with Prof. Waterston on "A comparative study of the grey and white matter, of the motor-cell groups and of the spinal accessory nerve, in the spinal cord of the porpoise."

Hepburn was a man of wide interests and took great pleasure in the study of natural history, and his home in Cardiff contains a valuable collection of deer antlers; he was a good artist and spent much of his holidays painting. He was a Knight of Grace of the Order of St John of Jerusalem (and was the Treasurer of the Cardiff division of that Order).

Hepburn came to Cardiff from that great School of Sir William Turner and, as an all-round anatomist, a great teacher, a clear speaker with a fine and well-trained voice, and great skill as a draughtsman, he was a worthy son of the Edinburgh School. But more than this, he came to Cardiff with the character of being a kindly, courteous and friendly gentleman who had won the affection of his colleagues and the love and admiration of many hundreds of his students. This was the reputation he brought to Cardiff twenty-eight years ago—a high

one to live up to—but one which Hepburn did not belie. His old students in Cardiff speak of him as a wonderful teacher and a real friend and the affection and regard which was felt for him was marked, just a month before his death, by a dinner in his honour, at which he was presented with a parchment and a sum of money; almost the last business in which Hepburn was engaged was the allocation of this money towards a medal, to be known as "The David Hepburn Medal," to be awarded to the best student in Anatomy, Histology and Embryology in the B.Sc. examination of the University of Wales. The Anatomical Department testifies in numerous diagrams to his skill as a draughtsman, and the various records in the Department and the Dean's Books, when Hepburn was in office, show his careful and orderly mind; while the general feeling of sorrow throughout the College and the city are eloquent tributes to the regard and affection which was felt for him.

For many, a gap has been made by his death which will not easily be filled.

C.M.W.

LIST OF BOOKS, PAPERS AND ADDRESSES BY PROF. DAVID HEPBURN

Books.

Anatomical articles for *Chambers' Encyclopaedia* (in 10 vols.).

Revisal of anatomical descriptions in Prof. Spence's *Lectures on Surgery*.

Revisal of anatomical descriptions in a "Text-book of abdominal Surgery," by Mr Skene Keith, assisted by George Keith, M.B.

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"The true shape, relations and structure of the alimentary viscera of the porpoise (*Phocoena communis*), as displayed by the Formal method." *Trans. Roy. Soc. Edin.* vol. XL, part 2.

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REVIEWS

Leonardo da Vinci, the Anatomist. By Prof. J. PLAYFAIR MCMURRICH. (Published for the Carnegie Institution of Washington by the Williams and Wilkins Co.) Very completely illustrated. $6·00.

The anatomical researches of Leonardo da Vinci will ever, we may presume, possess a deep and special interest for the student of anatomy. The fame of the master and the romantic history of his manuscripts, written and illustrated by his own hand, are sufficient in themselves to secure this. There is, however, a further and crowning interest in that the manuscripts are not in the form of a finished text-book, but rather in the form of rough notes—*obiter dicta*. We thus have, as we study them, the extraordinary privilege of watching step by step the mental processes of one of the most gifted and inspired of men as he attacks with little or no assistance from his predecessors, with none of the adventitious aid which modern science so freely gives, the fundamental and age-long problems of human anatomy and physiology, problems of which we, children of a later time, are largely in possession of the solution.

That Leonardo was at a certain period of his life engaged on anatomical researches, was well known to his contemporaries. Perhaps the earliest and most explicit reference occurs in an account of a visit paid to him in October, 1517, shortly before his death, by the Cardinal of Aragon at the Manor House of Cloux ("il palazzo del Clli," as Leonardo himself called it), which still stands on a quiet road running under the walls of the Château d'Amboise.

After Leonardo's death—but not until after the death of his devoted pupil and companion, Francesco Melzi—the manuscripts were dispersed, most of the anatomical ones finding their way into the English Royal Collection which Prince Charles, later Charles I, was engaged in founding. At the sequestration of the estate of Charles under the Commonwealth these manuscripts either escaped notice or were considered of little worth. No further mention of them occurs until 1784 when Dalton, the Librarian of George III, discovered them in a cabinet at Kensington Palace and brought them to the notice of William Hunter—not John, as Professor McMurrich states (p. 68).

Soon selections from the manuscripts began to appear, associated with the names of various authors, Chamberlaine, Sabachnikoff, Piumati and Rouveyre: finally, in 1911–16, the Quaderni d'Anatomia, edited by three distinguished members of the University of Kristiania in six folio volumes with transcriptions from the mirror-writing which Leonardo affected and with literal English and German translations, brought the publication of the manuscripts to a final and brilliant conclusion.

The books above mentioned are both rare and expensive and not within easy reach therefore of the student. The time was clearly propitious for the appearance of a single volume which would not merely supply an adequate summary of Leonardo's work and methods but also provide as a background a general account of the knowledge of his age.

Fortunately the idea of giving assistance in this direction occurred to the directors of the Carnegie Institution, who were able to enlist for the purpose the interest and service of Professor McMurrich than whom we venture to say, as scholar, anatomist

and educationalist, no better choice could possibly have been made. The result of this admirable co-operation is to be seen in the handsome volume under review.

The book opens with chapters devoted to the history of anatomy and of anatomical illustration, to the history of Leonardo himself and of his manuscripts, chapters eloquent of Professor McMurrich's erudition and literary charm. These are followed by chapters in which the subject is treated, system by system, in a manner which, it is interesting to note, closely follows what Leonardo himself had designed. In some ways the most interesting chapter is that devoted to Leonardo's methods, in which it is clearly demonstrated that Leonardo, at any rate in theory and we believe in no small measure in practice, was conversant with the various methods which even up to our own time have been introduced into anatomical teaching and investigation—dissection, sections, embedding, wax modelling, the experimental method, references to comparative anatomy and embryology: for it is in the originality and thoroughness of his methods that he most transcends his contemporaries.

A warning, however, should here be sounded against the acceptance as accomplished fact of all that appears in the manuscripts, for these, as we have already mentioned, are largely sheets of notes in which any idea or impression, however vague, might reasonably be recorded. We confess, for example, to considerable hesitation in believing that Leonardo succeeded in injecting with melted wax the lateral ventricles of the brain through either the third or fourth ventricle: the nature of the brain substance and the instruments available make this in our opinion highly incredible. We are inclined to think that we are here in the presence merely of a suggestion, on a par with that of inserting a piece of glass into the wall of the heart to watch the movements of the valves. It is true that Leonardo gives a figure of the lateral ventricles, but this is so crude as to require no knowledge other than what might be easily acquired by dissection.

Apart from such slight divergence of opinion in interpretation, we have nothing but unqualified and unstinted praise for the tribute which Professor McMurrich and the Directors of the Carnegie Institution have paid to the most distinguished of our line. It is no small satisfaction to feel that justice has at last been done, that the great Florentine has at last received the reward of his labours!

A Junior Course of Practical Zoology. By A. Milnes Marshall and C. H. Hurst. Revised by H. G. Newth. (London: John Murray.) 1930. 11th edition. Pp. xliii + 519 and 94 text-figs. Price 12*s.* net.

The first edition of this book appeared in 1887. During the forty-four years that have elapsed since then it has passed through eleven editions, two of which were reprinted, and has been revised by two editors. The present edition only differs from the last in minor points and no new types have been introduced, with the exception of a short paragraph on *Nyctotherus* and *Balantidium*. Nevertheless it has been revised carefully throughout and re-indexed. This will be a source of relief to all those teachers who consider this book the almost ideal and certainly the standard laboratory manual of zoology in English. No other book can, in our opinion, compete with this as a book of practical instruction in animal morphology for use in the laboratory. It is adapted to the requirements of University Intermediate Science and first year Medical Classes and is equally suitable for use in those schools where a serious attempt is made to teach the principles of zoology. To those who teach zoology and do not know this book, if there be any such, we can heartily recommend it.

F. W. R. B.

Anatomy in the Living Model. By DAVID WATERSTON, M.A., M.D., F.R.C.S.E., F.R.S.E., Bute Professor of Anatomy in the University of St Andrews. (London: Hodder and Stoughton Ltd.) 1931. Pp. 255. 16 plates and 74 figs. Price 25*s.* net.

Anatomy of late has striven with some success to clear itself from the charge that it was concerned only with the dead, and the appearance of such a book as this is to be warmly welcomed. Its professed aim, to be not merely a compendium of "surface anatomy" but a guide to the demonstration of structure and function in the living, is fittingly complementary to the spirit of the "James Mackenzie" Institute for Clinical Research, to which the author is an Hon. Consultant.

The first section, which deals with the skin-covered surface of the body in general, is the best and most novel part of the book. The consideration of the skin as a sense organ reflects the original work of the author in this field. The mention made of the problems connected with arterial cutaneous areas stimulates the desire for a fuller discussion of them.

The remaining sections deal with the parts of the body in turn. In each section a study of the surface contour of the part is followed by accounts of such matters as cutaneous nerve areas, the function of muscles and joints, and the surface projection of deep structures.

A series of short appendixes outline practical exercises such as the study of finger-prints, the demonstration of capillaries in living skin, and the electrical stimulation of sensory and motor nerves.

In a book of this type, some liberty in selection of subject-matter must be allowed. But obvious inconsistencies should be avoided, as when in the section on Upper Limb the statement, that the motor distribution of spinal segments is not described because no means are known for its determination in the living, is preceded by a brief account of the lymphatics of the limb and succeeded by an account of the main arteries which gives the diameter of each in millimetres. Nearly a page about the auricle is followed by two lines on the external auditory meatus (instrumental examination of ear and eye is deliberately excluded); no mention at all of the mastoid antrum was found in text or index. The enumerations of the surface "regions" of the B.N.A. might well be omitted as useless. The description of the action of the shoulder joint is hardly up to date; and in dealing with the knee joint the importance of the tonus of the surrounding muscles, so much stressed by the orthopaedic surgeon, is not brought out. In several places the balance of importance between muscles and ligaments is scarcely held true to modern conceptions. A general section on joint function and the group action of muscles might have been included with advantage. The level of the upper epiphysial cartilage of the humerus is stated to be at the "surgical neck." The medial border of the great toe is still said to be in the same straight line as the medial border of the foot, in contradiction of nature and Wood-Jones. These are some points noted for attention in the future editions which we hope will be called for.

A word must be said about the series of coloured plates which illustrate the sections on head and trunk. These were made with the aid of a dioptrograph from dissections at successive depths; tracings made from them can be superimposed. They are beautifully drawn and reproduced, but why include them in a book on the anatomy of the living? A few good radiograms of joints and of the stomach and duodenum would have been much more appropriate. The stomach and intestines are necessarily shown in the cadaveric position; this, in spite of ample recognition in the text of the findings of R. O. Moody, is specially unfortunate in a book of this order. And the plates are probably responsible for the rather high price of the volume, which we regret; for no avoidable obstacle should be put in the way of the use of such a book by medical students, who as yet, alas! too often lack the stimulus to acquire it which further evolution in "examination" anatomy will soon, we hope, provide.

Das Pollersche Verfahren zum Abformen an Lebenden und Toten sowie an Gegenständen. Von POLLER, E. B., und FETSCHER, E. Berlin und Vienna: Urban und Schwarzenberg. 1931. Pp. xii + 216. 129 illustrations. Abformen, geh. RM. 12.— geb. RM. 14.

This discussion of casting is as thorough as its scope of interest is all-inclusive: for doctors, dentists, anthropologists, criminologists, museum technicians, prehistorians, artists, teachers of handicraft, and laymen in general.

The authors consider the problem of plaster casting under two main heads: the impression of the model as a *negative*; and the formation of this negative into a *positive*. Each has its special technique, and more particularly a special medium of expression. For the former Poller has produced substances known as "Negocoll" and "Dentocoll" (the last for dental work only). This material is applied with a brush and upon hardening is resilient enough to be taken off in one piece, or at the most very few pieces. It records details with photographic accuracy, permits of exact duplication, and necessitates little or on preparation of the model used. For the positive Poller uses materials known as "Hominit" and "Celerit," specifically designed to register the details transmitted by the negatives.

The article covers the entire range of possibilities in casting portions of the human body, outlining the tools utilised, the steps in the procedure, and even offering a plan for the establishment of a working laboratory. With respect to the production of anatomical models, the casting of such a delicate organ as the brain is handled with consummate skill and almost unbelievable accuracy of result.

All workers engaged in casting reproduction of any sort must find in this article the lexicon of their science. More than that it holds promise of an efficiency and ease of reproduction hitherto deemed impossible.

Baillière's Synthetic Anatomy. By J. E. CHEESMAN. Part VII. The Thorax. Part VIII. The Abdomen. (London: Baillière, Tindall & Cox.) 1930. Price 3*s*. each.

These two parts now issued complete the survey of the body in this Atlas in vertical planes. As the successive planes proceed in a slightly oblique direction from front to back, an enhanced idea of antero-posterior depth, simulating a stereoscopic effect, is ingeniously conveyed. The plates in Parts VII and VIII are so bound that they can be interlocked in register in order to provide a representation of the whole trunk. The accuracy of anatomical relationships commented on in reviewing previous parts is well maintained, although the origin of the portal vein is placed too high with reference to the pancreas.

The publishers state that the Atlas will end with the issue of three additional parts, Brain and Male and Female Perinaeum, portrayed in horizontal sections.

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